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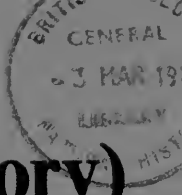|	
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Synopsis

The slides of freshwater naked amoebae prepared early in this century by Eugène Penard have been examined with modern optical systems, and much of the material is presented in photomicrographs. The new genus *Thecochaos* is proposed for amoebae which resemble *Thecamoeba* except in being multinucleate, with *T. fibrillosum* (Greeff, 1891) as the type-species. Other new combinations include *Chaos nobile* (Penard, 1902), *Thecamoeba papyracea* (Penard, 1905), and *Thecochaos album* (Greeff, 1891). The validity of several named species of *Pelomyxa* is considered without a definite conclusion. The taxonomic positions of several species cannot be determined on the basis of the present material.

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Introduction

Eugène Penard (1855–1954) was one of the classical students of protozoan natural history. From 1887 until his eyes failed him in 1922, he investigated diverse Sarcodina, ciliates, and flagellates, all collected from natural sources and studied alive and in fixed preparations. Most of his life was spent in his native Geneva, but his publications include material from such far places as Loch Ness, Sierra Leone, the Rocky Mountains, and the Himalayas. To the biography by Deflandre (1958) are appended a list of publications and a list of 24 genera and 426 species of Protozoa (including 31 species of Gymnamoebia) erected by Penard.

Altogether Penard produced at least 82 protistological publications, the great majority on Sarcodina. His most important work on rhizopods, including naked amoebae, is *Faune Rhizopodique du Bassin du Léman* (1902), foreshadowed by his 'Étude sur les Rhizopodes d'eau douce' in 1890. The *Faune Rhizopodique* is among the classical publications on naked amoebae, which also include those of Leidy (1879), Cash (1905), Cash & Wailes (1919), and Schaeffer (1926). All except the last also deal with testaceans, which indeed take up the larger part of the space.

Penard was interested especially in observations of living organisms, considering such 'physiology' more interesting and more important than systematics, which he did, however, regard as essential. Amongst the characters which he could observe in naked amoebae, he considered the nucleus especially important. To preserve his organisms and facilitate observations of such characters as the nucleus, he made many permanent preparations. His standard method (Penard, 1902) was fixation with absolute alcohol, staining with borax carmine, and mounting in Canada balsam. His observations were made without an immersion objective (Deflandre, 1958), and of course he depended on drawings rather than photographs to convey visual impressions. Deflandre praised these drawings highly, though it must be said that in the case of Gymnamoebia one might often wish for more details, more depth, and especially more individual amoebae. The subsequent reproduction by later authors of a single Penard drawing per species, which even if composite in origin could only represent a single cell at a single moment, has over the years proved inadequate for identification.

According to Deflandre (1958) Penard's slides are preserved in three major collections. When Deflandre was writing (he died in 1973), the smallest of these three main collections was in his own possession. It comprised 280 slides, of which 233 were of rhizopods, including 18 slides of *Amoeba* (in Penard's broad sense of the genus) and five of *Pelomyxa*. The second collection was at the Muséum d'Histoire Naturelle of Geneva, containing 663 preparations, according to Deflandre. In 1952 Deflandre found these preparations in good condition but could not summarize their contents for lack of an adequate catalogue. However, Grospietsch (1975), in a publication with limited distribution, listed 791 slides in the Geneva collection. These include 48 slides of 13 species of *Amoeba* (in Penard's broad sense) and 11 slides of five species of *Pelomyxa*. All these species of naked amoebae except two of *Amoeba* are also represented in the third and largest major collection, that at the British Museum (Natural History), consisting of 950 slides. The great majority of these are testaceans. The 55 slides in this third collection bearing naked lobose amoebae (Gymnamoebia) are the object of the present study. According to Penard's nomenclature, they contain specimens of 20 species, as well as one slide with no specific identification.

Besides the three major collections, Heal (1965) lists three smaller collections of Penard's slides in Britain, but these contain only three of Penard's species of Gymnamoebia, all represented in the collection at the British Museum (Natural History).

There are several reasons for re-examining Penard's slides now. Free-living amoebae are much better known than they were a few decades ago. They have been investigated by more workers with a greater diversity of aims than ever before, applying modern tools. Knowledge of taxonomic value has been developed in some cases by workers who initially had no particular interest in taxonomy. It is principally large amoebae which have been much used in cell biological investigations, with the exception of *Acanthamoeba*, and Penard's

publications dealt with and his slides preserve mainly larger amoebae. Among the Penard material are represented several groups whose taxonomic status and boundaries are still matters of some uncertainty. For example, how many species of *Pelomyxa* did Penard actually have in front of him? There are also organisms which apparently have been seen by few other workers, so that on the basis of Penard's text and few drawings their existence and identification have been questioned: Are there, already described and identifiable, more species of *Chaos* than the two familiar to present-day cell biologists? Are there multinucleate amoebae which resemble *Thecamoeba* more than they resemble *Amoeba* and thus perhaps should not be classified as *Chaos*? With modern optical and photographic equipment, the Penard material can provide answers to some questions and give information for further consideration of those questions which remain unsettled.

Bright field, phase contrast, and differential interference contrast optics have been used to examine and photograph the preparations. In most cases, it was possible to examine and photograph the slides with an objective up to × 63 (giving × 800 final magnification for direct observation, × 315 on the photographic negative). In a few cases the thickness of the mount made use of an objective greater than × 10 impossible, but enlargement of the negatives provided further information, such as nuclear size and structure. Most of the material on the slides was photographed, the omissions being a very small quantity of useless material and some repetitive material. The same cells were usually photographed at two magnifications and with at least two optical systems. From these hundreds of photomicrographs, the most informative are included as illustrations. The optical systems are not consistent amongst the illustrations, since the most informative photomicrographs of one species or feature were not always obtained with the same system which was most useful for another. That this inconsistency does not prevent useful comparison can be seen by examining, for example, the figures of *Amoeba fibrillosa* and those of *Amoeba alba*.

All reasonably intact cells were measured. In uni- or binucleate species, all discernible nuclei were measured. In multinucleate cells, 25 nuclei were measured (if that many were present) in one or more cells.

Finally, it should be noted that Penard's over-all taxonomic system for rhizopods was simple and imprecise (Penard, 1902). He recognized two 'groups', the Lobosa and the Reticulosa, with the Filosa as a subgroup of the former. Within the naked lobose amoebae he classified most in the genus *Amoeba*, although he also used the two supposedly anucleate genera *Protamoeba* Haeckel, 1866, and *Gloïdium* Sorskine, as well as *Dinamoeba* Leidy, 1874, which is still recognized. He considered a subdivision of the genus *Amoeba sensu lato* premature at that time. *Pelomyxa* he defined as 'Amibes à mouvements lents, toujours pourvues de bactéries symbiotiques'. A modern classification of as many of Penard's organisms (on these slides) as possible will be suggested.

Observations

These are in no sense species descriptions but only summaries of the information derived from the slides. Because of the limited taxonomic usefulness of fixed light-microscopical preparations of Gymnamoebia (greater for these larger amoebae than for smaller ones), a fuller picture of the organisms requires consultation of the descriptions of living amoebae in the *Faune Rhizopodique* (1902) and Penard's other publications. It will be found that the measurements given in that publication differ somewhat from those derived from the fixed preparations. For some species listed here, Page (1976, 1977) gives more complete information, under modern generic names. The headings below use Penard's generic classification; some re-classifications with gender modifications of specific epithets are proposed later in this publication. The authorships given in the headings are those required by today's nomenclatorial regulations whether or not they correspond with those used by Penard. Dates are absent from many slides. All slides bearing dates of preparation were made between 1901 and 1903, but it is almost certain that some were made later. The first two digits of the slide numbers indicate the date of deposit in the British Museum (Natural

History): ·04 = 1904, etc. All these slides bear material collected in Geneva and vicinity, including Haute Savoie.

Fixation is as one would expect given the use of absolute alcohol alone, with some shrinkage of conical subpseudopodia (*Amoeba vespertilio* and *Dinamoeba mirabilis*) and blurring of the distinction between hyaloplasm and granuloplasm. The nuclear stain remains good. Most of the amoebae are located near the centres of the preparations. Some cells are broken. Only a minority of the amoebae are in the form taken during steady locomotion, with more irregular forms, e.g., producing branches in several directions or spreading on the substratum, common.

The references under each species heading list the publication(s) in which Penard described each species, since it is only his material which is being considered here. Publications of other authors are cited in the remarks where relevant.

Amoeba proteus Leidy, 1878
(Figs 1–6)

Penard, 1902, pages 57–60

SLIDE NUMBERS. 04.5.9.19; 04.5.9.30; 20.12.8.10 (labelled *Amoeba laureata* with notation 'avec 1 *Amoeba proteus*'); 20.12.8.15; 20.12.8.16; 20.12.8.17; 20.12.8.18.

TOTAL NUMBER OF AMOEBAE. 13.

DESCRIPTION AND REMARKS. Several of these cells had the elongated form often seen in more rapid locomotion of *A. proteus*, the longest (Fig. 1), 524 μm long, with a second pseudopodium which may have been undergoing retraction at the moment of fixation. These preparations were examined in the light of Schaeffer's (1916) statement: 'I therefore suggest the specific name *dubia* for the organism named *proteus* by Penard.' None of the amoebae in these preparations had a cell form not reconcilable with that of *A. proteus* as understood since Schaeffer's (1916) more precise definition of that species, though one could equally say that these shapes could also be encountered in *Polychaos dubium* (Schaeffer, 1916). Certainly the three locomotive forms on slide 20.12.8.15 are fully compatible with *A. proteus*. Schaeffer pointed out the inconsistency between the discoid nuclear shape described for *A. proteus* by Leidy (1879) and that which Penard described as 'toujours ovoïde' except in a variety where it was 'toujours parfaitement globuleux'. The nuclei in most of Penard's specimens could indeed be ovoid, but at least one of those on slide 20.12.8.15 is discoidal (Figs 1, 4), and all the amoebae on that slide appear to be of the same type. Nuclear diameters in Penard's specimens are 27·5 to 54 μm, with only one below 37 μm.

Although it is therefore possible that some of Penard's slides labelled '*Amoeba proteus*' do bear members of other species, according to present specific distinctions, the amoebae on slide 20.12.8.15 certainly correspond to *A. proteus*. One or two amoebae on that slide appear to have the surface ridges which Schaeffer made diagnostic of *A. proteus*, though care is necessary in evaluating ridges or folds on these preparations. The slide 20.12.8.17, with the notation 'Variété', bears an amoeba which could be a *P. dubium* if any of these are (Fig. 3).

Most of these amoebae contain ingested diatoms, and a few other algae and possible protozoa were seen in some.

Amongst these slides is one, 20.12.8.18 ('avec prolongements cryptogamiques') with a single amoeba trailing a tuft of filaments (Fig. 5). These presumed hyphae (Fig. 6) are apparently nonseptate and about 2·5 μm in diameter, and the longest extends about 74 μm from the amoeba. Slide 04.5.9.19 is a preparation of an amoeba 'écrasée pour montrer les parasites'. These filaments are apparently nonseptate, with a diameter up to 3 μm or slightly more. In both cases, Penard's notation (not taxonomic label) refers to the '*Ouramoeba*' of Leidy (1879), now generally acknowledged to have consisted simply of such infected members of the genus *Amoeba*.
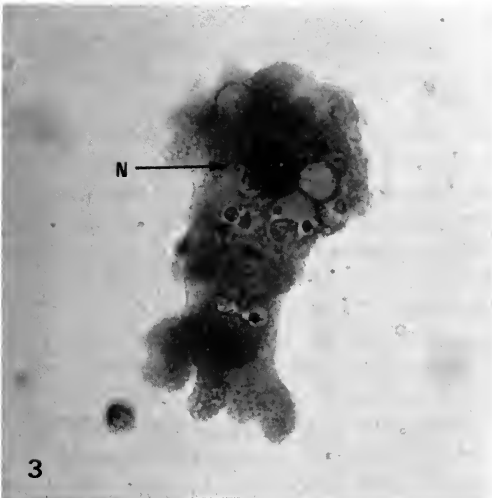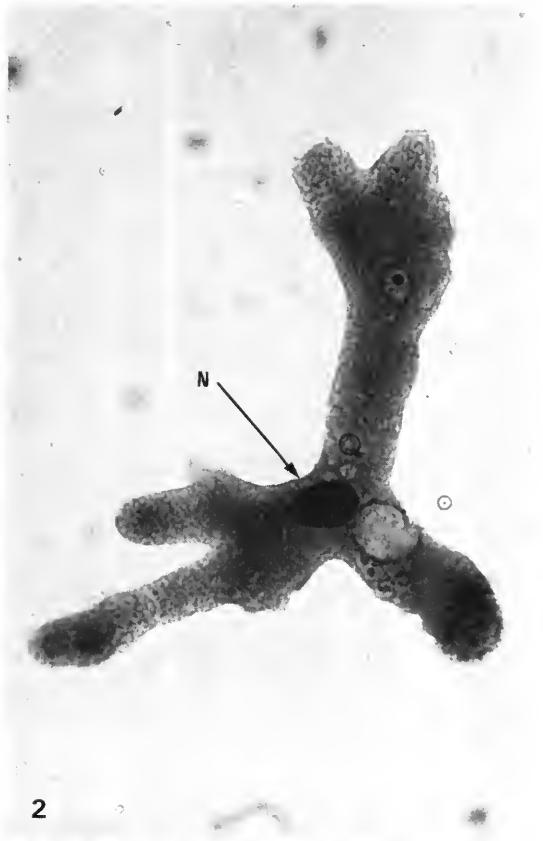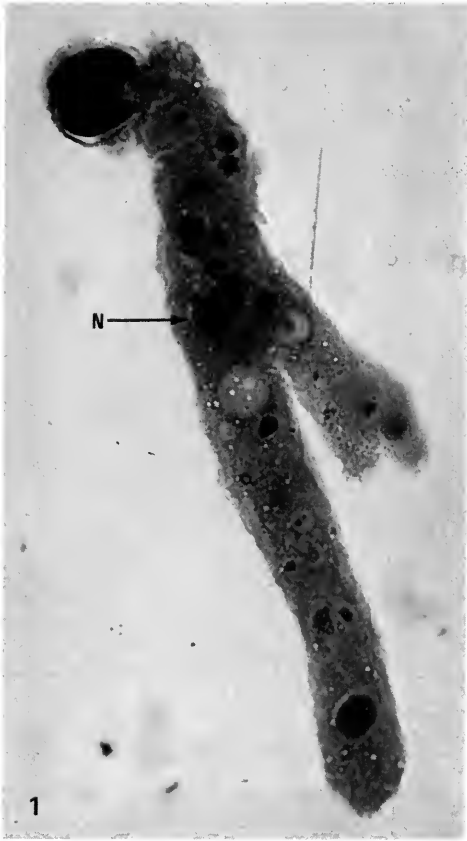
Figs 1–4 *Amoeba proteus.* (1) to (3) Whole cells × 200. (4) Nucleus × 1000. N = nucleus.
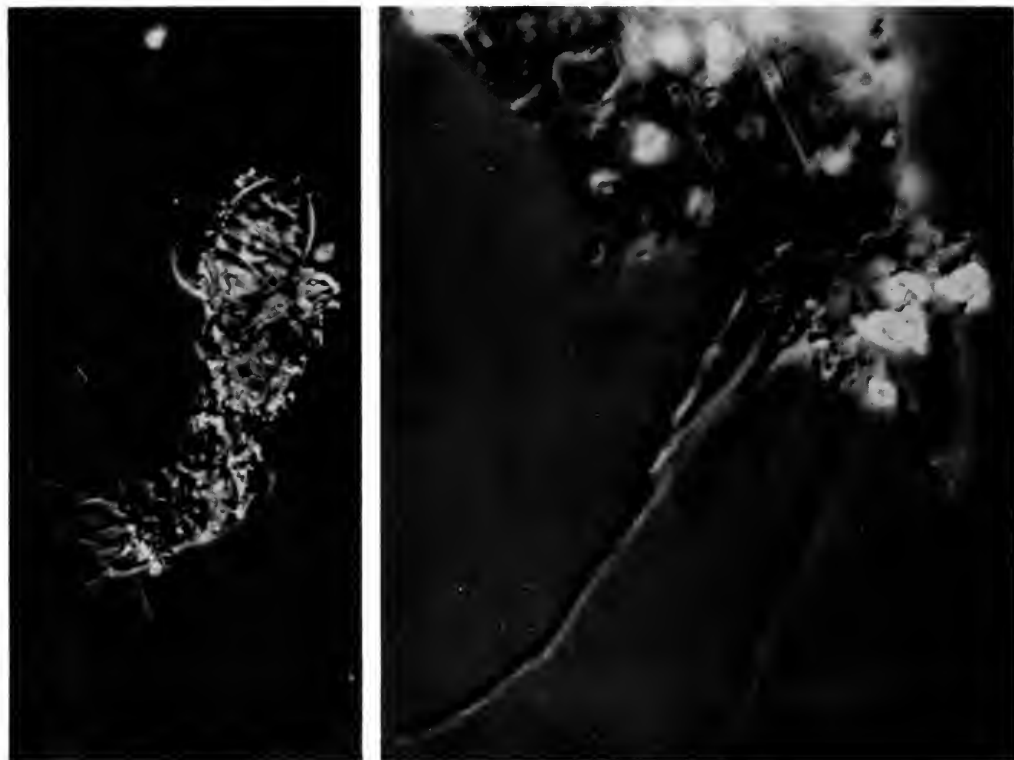
Figs 5, 6 *Amoeba proteus* with apparent fungal parasite. (5) × 250. (6) × 1000. D = diatom. F = fungal hyphae.

Amoeba nitida Penard, 1902
(Figs 7–11)

SLIDE NUMBERS. 04.5.9.23; 04.5.9.24; 20.12.8.12; 20.12.8.13.

TOTAL NUMBER OF AMOEBAE. 8.

DESCRIPTION AND REMARKS. At least four of these amoebae are in an elongate locomotive form (maximum length 408 μm) with one main pseudopodium, though some pseudopodia are found as separate fragments. In four amoebae (one binucleate) the nucleus is distinctly discoid (Figs 9, 10). Although the angle of viewing makes the other nuclei appear roughly circular or, in one case, oval in outline, a closer examination suggests that these nuclei, too, are discoid. The thickness is about half the greatest diameter or even less. The irregular outline of the nuclei in flat view (Fig. 11) recalls Penard's (1902) emphasis on the foldings and invaginations to which the nuclear envelope is susceptible. The nucleolar spherules are arranged in a layer just beneath the nuclear envelope, but in several nuclei there is also a central mass, perhaps a fixation artifact. The maximum diameters of nuclei in the uninucleate amoebae were 34 to 54 μm; the maximum diameters of the nuclei in the binucleate amoeba were 35 and 31 μm.

Ingested material included diatoms and possibly a few protozoa. At least one amoeba contained crystals, which appeared to be truncate bipyramids, though they were somewhat deteriorated.

Schaeffer (1916) asserted that Penard's *A. nitida* was equivalent to the *A. proteus* of Leidy (1879). My examination of Penard's slides labelled '*Amoeba proteus*' (see previous section) showed that the amoebae on at least one of them could not be *Polychaos dubium*, with which
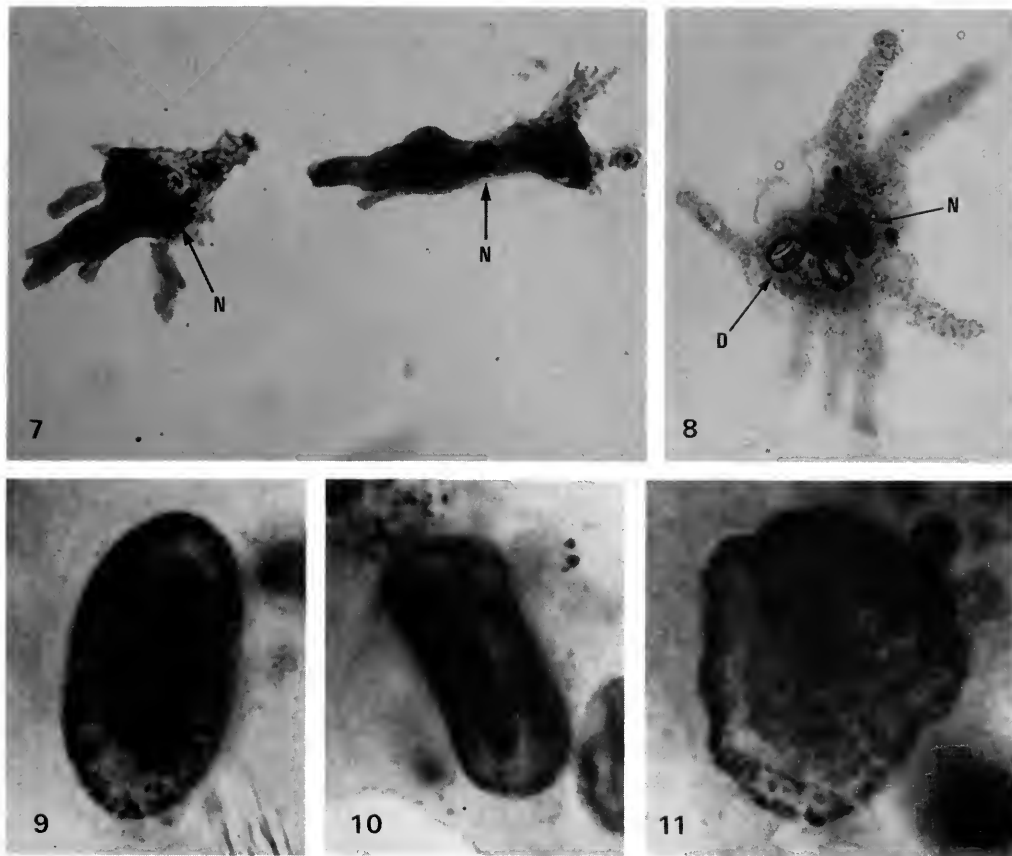
Figs 7–11 *Amoeba nitida* (= *A. proteus*). (7), (8) Whole cells × 200. (9) to (11) Nuclei × 1000. D = diatom. N = nucleus.

Schaeffer (using the name *Amoeba dubia*) equated the amoebae described by Penard (1902) as *A. proteus*, even if some of Penard's '*Amoeba proteus*' might not belong to the latter species as now defined. However, on the basis of these preparations as well as Penard's text, I accept Schaeffer's view that *A. nitida* is a junior synonym of *A. proteus*. The deformability of the nuclear envelope in '*Amoeba nitida*' is not a strong enough character for a specific separation. To separate the species on that basis would require isolation of a strain identifiable as *A. nitida* and demonstration that this deformability, leading to marked infolding and invagination, rests on an ultrastructural difference from the nuclear envelope of *A. proteus* (Flickinger, 1974).

Amoeba sp.
(Figs 12–15)

SLIDE NUMBER. 20.12.8.30.

TOTAL NUMBER OF AMOEBAE. 2.

DESCRIPTION AND REMARKS. This slide bears Penard's comment: 'Grande amibe à noyau curieux. L'un des individus renferme un petit rhizopode encore inconnu.' These amoebae (Figs 12 and 13) are 320 and 398 μm long. The nucleus (Fig. 14) has in each case an irregular outline, with maximum diameters of 46 and 49 μm. Careful focussing showed the thickness to be about half the greatest diameter or less, but the shape appeared to be lenticular rather
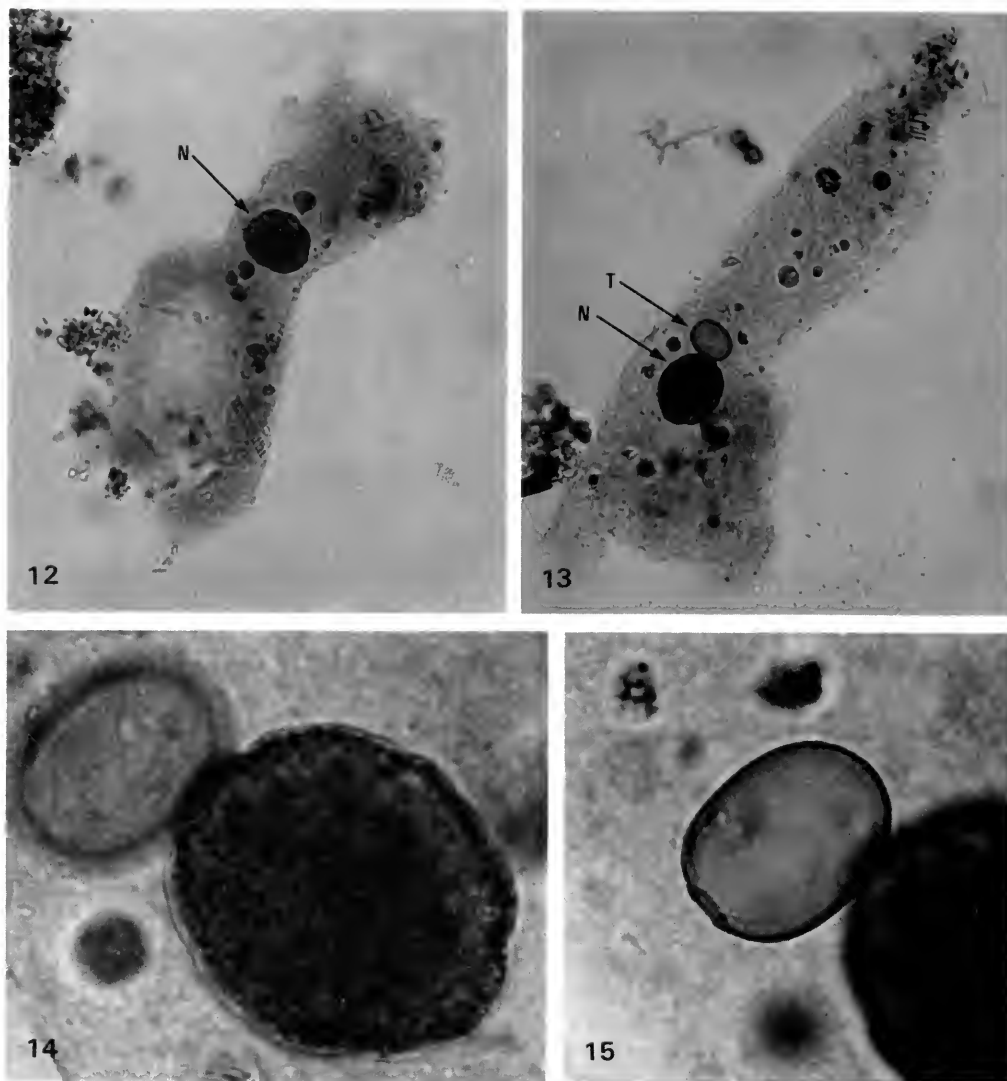
Figs 12–15 *Amoeba* sp. (12), (13) Whole cells × 200. (14) Nucleus, with rhizopod test out of focus × 1000. (15) Rhizopod test, with nucleus out of focus × 1000. N = nucleus. T = test.

than discoid. There is a peripheral layer of granules, each slightly more than 1·5 μm in diameter, just beneath the nuclear membrane, and a less distinct, large central mass, which appears granular. Both amoebae contained ingested diatoms; one contained the test (Fig. 15) to which Penard's note refers (29 × 22 μm); and both contained what appeared to be small protozoa, which in one amoeba include apparent ciliates.

Given the difficulty of judging from fixed preparations alone, one cannot identify these amoebae with certainty, though they seem to be either *Amoeba* or *Polychaos*.

Amoeba nobilis Penard, 1902
(Figs 16–21)

Slide numbers. 04.5.9.21; 04.5.9.22; 20.12.8.14.

Total number of amoebae. 7.
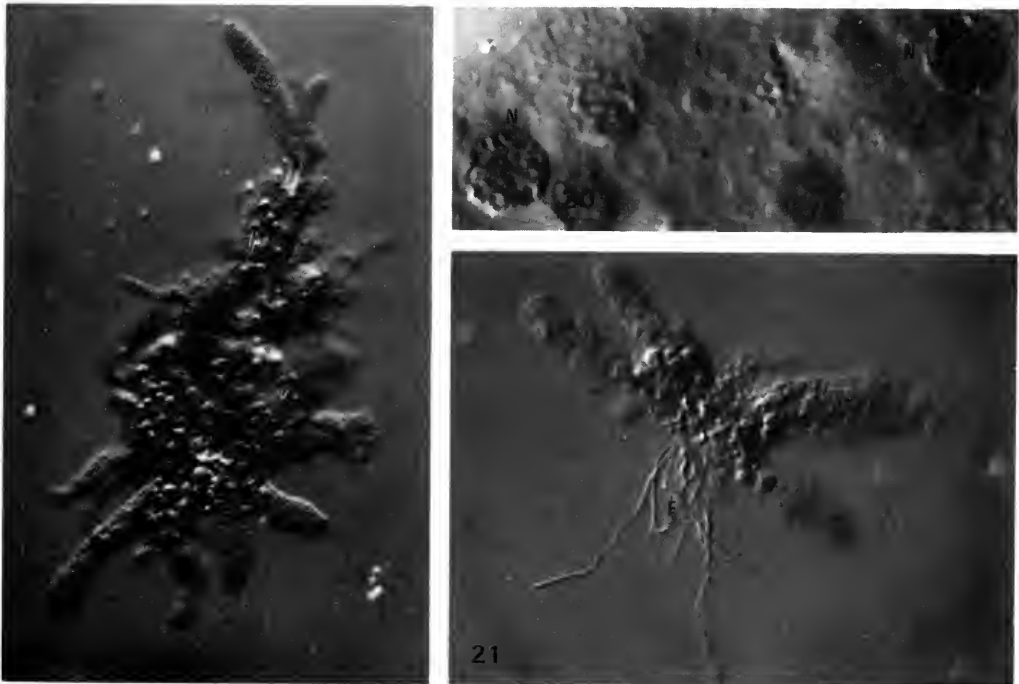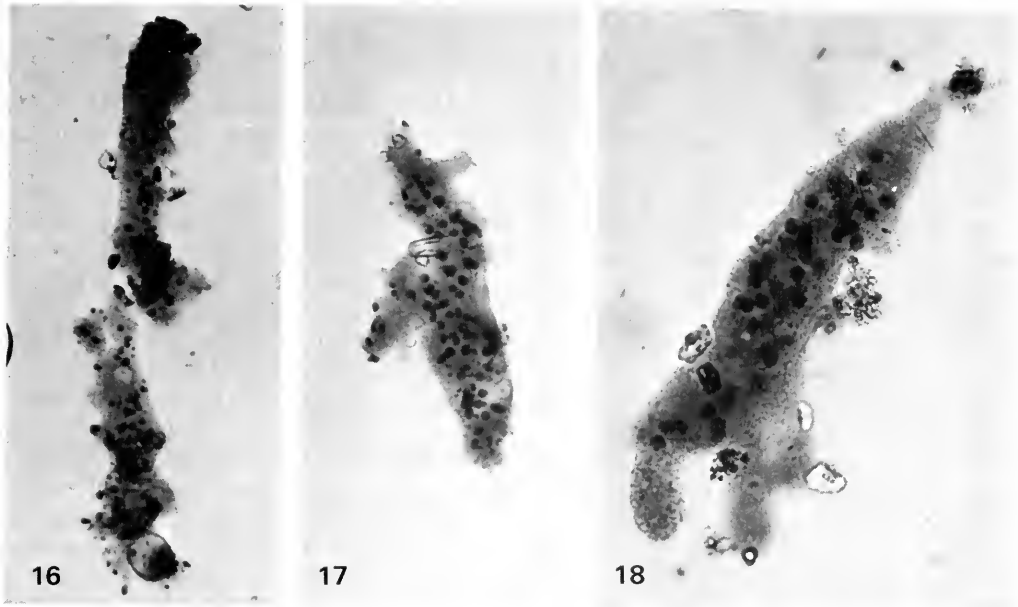
Figs 16–21 *Amoeba nobilis* (=*Chaos nobile* comb. nov.) (16–18) × 200. (19) × 150. (20) Nuclei × 1000. (21) Amoeba apparently infected by fungus × 200.

DESCRIPTION AND REMARKS. These are multinucleate Amoebidae. The five amoebae on slide 20.12.8.14 are in the locomotive form; their lengths are from 262 to 446 µm. The largest amoeba in these preparations, on slide 04.5.9.22 (Fig. 19) is not a locomotive form and has pseudopodia projecting in several directions, with its greatest dimension 524 µm across, so

that it would be much longer in locomotion; this resembles the cell described by Penard (1902) at the top of page 66. However, none of these fixed amoebae clearly shows the distal expansion of the pseudopodia pictured by Penard (1902) in Fig. 1 on page 66, which gives it the *Polychaos*-like appearance mentioned by Page (1976). It must be kept in mind that these fixed preparations undoubtedly do not show the pseudopodial form as accurately as do observations of live amoebae.

The number of nuclei counted in these seven amoebae ranged from 25 to 100 per amoeba, approximately, in the majority between 42 and 59, but these counts and those of other multinucleate species made from these slides are on the conservative side, since one cannot flatten the cells to observe all nuclei well. One hundred nuclei, 25 in each of four amoebae, had diameters ranging from 8·5 to 13·0 μm; the mean diameter varied from 9·8 μm in one amoeba to 12·2 μm in another. The nuclei (Fig. 20) are spherical to ovoid. The apparent nucleolar material is arranged in several small, irregular bodies on the inner side of the nuclear envelope, but there are also smaller granular bodies and filamentous material, apparently in the inner part of the nucleus.

Amongst the ingested material are diatoms and probably small protozoa.

One preparation, with the notation 'Avec cryptogames parasites', contains an amoeba, not in the locomotive form, with hypha-like filaments extending from one side to a maximum length of 184 μm from the amoeba (Fig. 21). Penard (1902) discussed this at some length.

Vonwiller (1913) isolated from an aquarium at Würzburg an amoeba which, after comparing his material with Penard's, he concluded was *A. nobilis*. Siemensma (1980) has found a similar amoeba in the Netherlands. Cysts have not been observed by these workers, although cysts are known to occur in the two recognized species of multinucleate Amoebidae, *Chaos carolinense* (Wilson, 1900) and *C. illinoisense* (Kudo, 1950) (Chapman-Andresen, 1979).

Amoeba nobilis, as seen in these preparations and in Penard's descriptions, is undoubtedly a member of the family Amoebidae as now defined (Page, 1976). It should therefore be known as *Chaos nobile* (Penard, 1902) comb. nov.

Amoeba laureata Penard, 1902
(Figs 22–24)

SLIDE NUMBERS. 20.12.8.9; 20.12.8.10 (also contains *A. proteus*).

TOTAL NUMBER OF AMOEBAE. 2.

DESCRIPTION AND REMARKS. Observations on this species were limited by the facts that only two amoebae were present and the thickness of the preparations did not permit use of an objective lens above × 10. Furthermore, neither of the amoebae is a normal locomotive form.

The amoeba on slide 20.12.8.9 (Fig. 22) is made up of two thick branches and a knobby posterior end. The cell surface is separated from the cytoplasm around much of the periphery of the amoeba and is somewhat wrinkled. However, a comparison with the second amoeba (Fig. 23) suggests that this surface may not be a *Thecamoeba*-like pellicle. Possibly the fixation method is responsible for the separation. The second amoeba likewise has two arms or branches, but much longer and slender, proceeding from a main mass which includes the more or less knobby uroidal region. These amoebae do not look like the one shown by Penard (1902) in Fig. 1, page 132, which is an *Amoeba proteus*-like locomotive form, although Penard states that such a form is very rare in this species. Nor is the villous character of the uroid, described by Penard for this species, discernible in these preparations, perhaps having been distorted in fixation.

The length of the thicker amoeba, from the posterior end to the tip of the main branch, is 310 μm. The greatest extent of the more slender amoeba, from the tip of one pseudopodium to the tip of the other, is 314 μm.

Although the conditions of observation did not permit a count of the nuclei, it is obvious that there are hundreds per amoeba. (Penard said that the number sometimes exceeds 1000.)
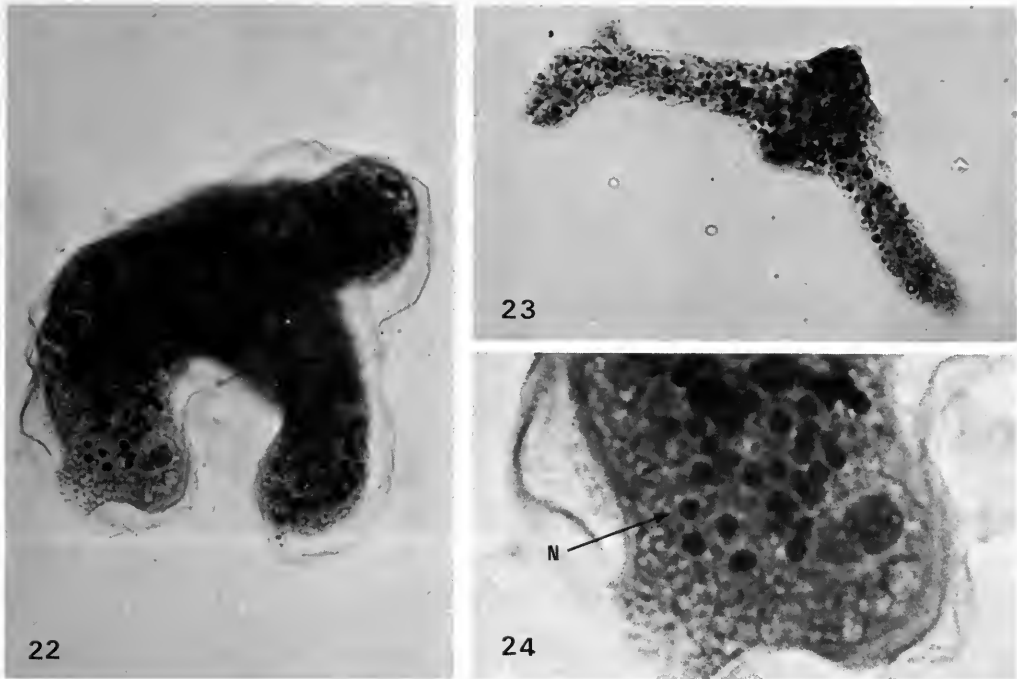
Figs 22–24 *Amoeba laureata.* (22), (23) Whole cells × 200. (24) Enlargement of amoeba in (22) to show nuclei × 500. N = nucleus.

The micrographs of the nuclei (Fig. 24) do not show their structure very distinctly, but denser patches around the periphery suggest that many of them have the structure shown by Penard (1902) in his Fig. 4, page 132, with presumed nucleolar material in a few small parietal bodies. The greatest diameter of a nucleus measured on these photomicrographs was about 6·5 μm, somewhat below Penard's figure of 8–10 μm, which appears to be derived from live material.

A few diatoms and possibly a few other unicellular algae were seen, but many inclusions were not identifiable because of the conditions of observation.

The taxonomic position of this species is probably not determinable from these preparations alone. The thickness of the amoeba in one preparation recalls *Pelomyxa*. However, the branching of these two amoebae is uncharacteristic of *Pelomyxa*. Furthermore, the possession of symbiotic bacteria was considered by Penard a characteristic of *Pelomyxa* and is so considered today (though bacteria occur in the cytoplasm of some Amoebidae). Penard explicitly mentions their absence in this species, which he would have classified as a *Pelomyxa* if he had found such endosymbionts. The presence of crystals, reported by Penard, also suggests that this is not a *Pelomyxa* (Griffin, 1961). Therefore, *A. laureata* may well be a *Chaos*; but the limitations of the available material make it advisable to reserve judgement.

'*Amoeba peritissima* Penard'
(Figs 25–27)

SLIDE NUMBER. 06.4.27.3.

TOTAL NUMBER OF AMOEBAE. 2.

DESCRIPTION AND REMARKS. These are thickly limax-shaped, multinucleate amoebae, if the two individuals available are representative. One cell measured 208 μm long by 68 μm broad; the other, 204 × 73 μm.
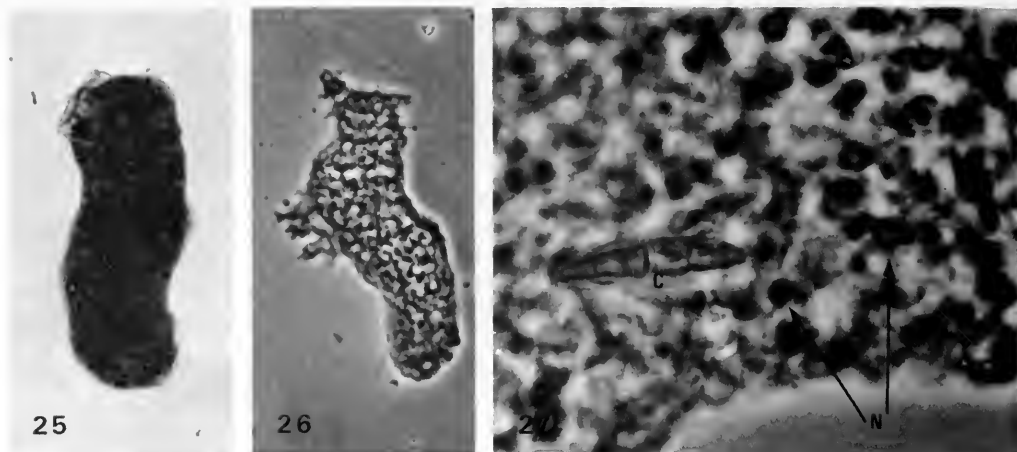
Figs 25–27 '*Amoeba peritissima*' (*nomen nudum*). (25), (26) Whole cells × 200. (27) Enlargement of part of amoeba in (26), to show nuclei. × 1000. C = conidium. N = nucleus.

Since the cytoplasm of one cell was less densely stained than that of the other, observations of nuclei were made on the former. This amoeba (Fig. 26) contained about 200 nuclei, on a conservative count. Observations of nuclear structure were not completely satisfactory. The nuclei (Fig. 27) appeared to contain a compact nucleolus, which at times appeared central and at other times eccentric in the nucleus. The central region of the nucleolus sometimes stained less densely than the outer part, leaving a lacuna. The diameters of 25 amoebae were 6·0 to 8·4 μm, mostly toward the lower end of that range.

One amoeba (Fig. 27) contained a multicellular conidium. The other (Fig. 25), which appeared to be ingesting an object at the time of fixation, contained several truncately bipyramidal crystals of sizes up to 12×9 μm.

Although this slide is labelled '*Amoeba peritissima* Penard', there is in fact no such specific name in the literature, and use of the name here is not intended as a publication to make it taxonomically available. It is a *nomen nudum*. A full taxonomic treatment would be possible only if this organism were found again and examined in sufficient numbers. Its generic position is uncertain. The thick limax form resembles *Pelomyxa*. However, the presence of crystals again suggests that it is not a *Pelomyxa* (Griffin, 1961). I can neither confirm nor rule out the presence of symbiotic bacteria on examination of these two preserved amoebae, but Penard's use of the generic name *Amoeba* indicates that he found no symbiotic bacteria. Again, this carefulness of Penard, who was familiar with diverse multinucleate amoebae, contrasts with the loose usage of some recent authors, who would throw all large multinucleate lobose amoebae into the genus *Pelomyxa* no mather how they differ in light- and electron-microscopical structure and in such basic physiological characters as locomotion and respiration.

Amoeba terricola Greeff, 1866
(Figs 28–33)

Penard, 1902, pages 104–121; 1905; 1913.

SLIDE NUMBERS. 20.12.8.20; 20.12.8.21; 20.12.8.22; 20.12.8.23; 20.12.8.24; 20.12.8.25; 20.12.8.26; 20.12.8.27; 20.12.8.28.

TOTAL NUMBER OF AMOEBAE. 16 (not including six of 'forme *papyracea*').

DESCRIPTION AND REMARKS. The slides designated as this species include one (20.12.8.25) with the notation 'forme *papyracea*' and another (20.12.8.28) labelled 'Variété'. As will be
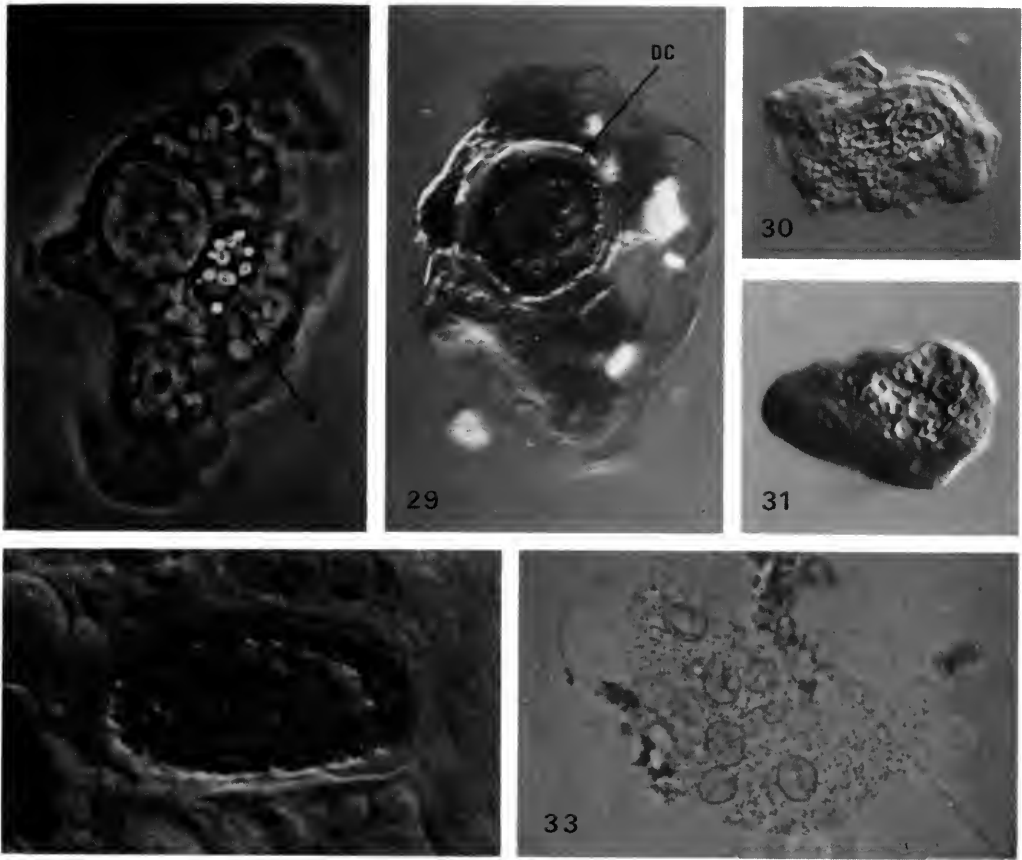
Figs 28–33 *Amoeba terricola* (= *Thecamoeba terricola*). (28) Whole cell × 500. (29) Amoeba with *Diplochlamys* in food vacuole × 200. (30) Whole cell × 200. (31) Whole cell labelled 'Variété' × 200. (32) Nucleus × 1000. (33) Bodies like collapsed sporangia or cyst walls in remains of amoeba, on slide labelled 'Parasitée' × 250. DC = *Diplochlamys*. N = nucleus.

seen below, this collection also includes one slide labelled '*Amoeba papyracea*'. Penard described the latter as a separate species in 1905, but in 1913 he decided to 'renounce' it and re-unite it with *A. terricola*. For the sake of clarity, the amoebae on slide 20.12.8.25 will be described under *Amoeba papyracea*, and the status of that species will be considered there. The present description is therefore derived from the amoebae on the other '*Amoeba terricola*' slides.

The maximum dimensions of these amoebae ranged from 94 to 262 μm, but most were 120 μm or more, and two of the smallest had been fixed 'après 32 jours d'isolement', in which time their size may well have decreased. The forms (Figs 28–31) were typical of *Thecamoeba*, though the majority did not appear to have been in locomotion when fixed, even if they were extended and flattened. The nuclei (Figs 28, 32) were the elongate ellipsoids or ovoids characteristic of the species, with a maximum length : breadth ratio of 2·3 and a mean of 1·7. In uninucleate cells (one was binucleate) the lengths of the nuclei were 24 to 55 μm (mean 34·7 μm), the majority between 24 and 38 μm. Elongate parietal nucleolar pieces, mostly at the ends of the nuclei as seen in living amoebae of the species (Page, 1977), did not stain well, in contrast to the presumed chromatin in the interior of the nucleus.

Identifiable ingested material included a few protozoa, including one identified by Penard as a *Diplochlamys* (Fig. 29) and a few small naked amoebae.
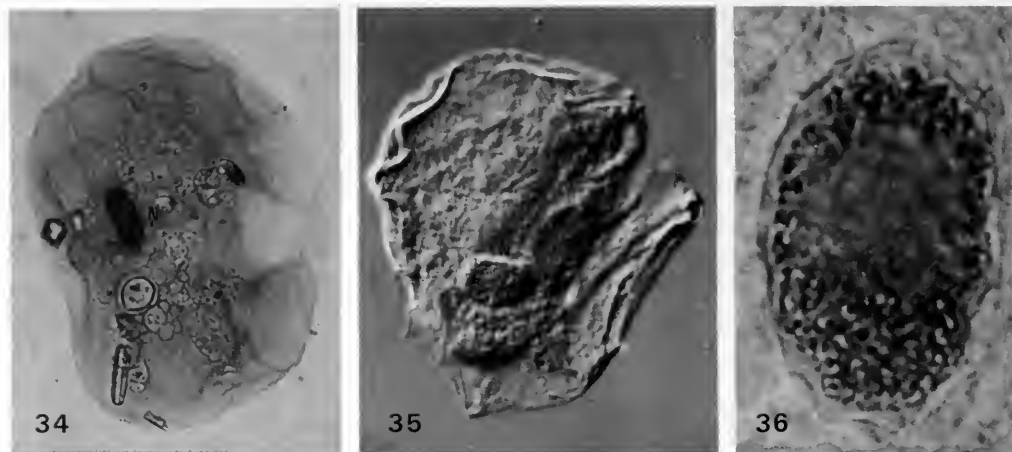
Figs 34–36 *Amoeba papyracea* (= *Thecamoeba papyracea* comb. nov.) (34), (35) Whole cells × 200. (36) Nucleus × 1000. N = nucleus.

One slide (20.12.8.21) bore the notation, 'Formation de petits kystes. Enveloppe déchirée.' The interpretation of this preparation is doubtful, which must be said also about 20.12.8.23, bearing the note, 'Parasitée' and containing bodies (Fig. 33) which may be empty fungal sporangia but could also be collapsed cyst walls of smaller amoebae.

The nuclei of these amoebae are somewhat larger than those found by Page (1977) in English strains of *Thecamoeba terricola*, but there seems little doubt that these amoebae and those investigated by other authors (comparison in Page, 1977) belong to the same species.

Amoeba papyracea Penard, 1905
(Figs 34–36)

Penard, 1905, 1913.

SLIDE NUMBER. 06.4.27.1 (see below).

TOTAL NUMBER OF AMOEBAE. one on above slide; six of '*Amoeba terricola* forme *papyracea*'.

DESCRIPTION AND REMARKS. Penard's change of mind about the specific status of these organisms has been mentioned under the preceding species. The description given here is derived from both the single amoeba on slide 06.4.27.1 and the six on slide 20.12.8.25, 'forme *papyracea*' of '*Amoeba terricola*'.

As Penard says in both publications on this species, the amoebae appear more hyaline and more transparent than the usual *A. terricola*. Both his descriptions and the appearance of the fixed amoebae suggest that they are somewhat less rigid. The lengths of these seven amoebae ranged from 192 to 233 μm; all but one were more than 200 μm long. The nuclear structure is as shown by Penard in both illustrations. The nucleus (Fig. 36) is an elongate ovoid or ellipsoid. Although Penard describes it as broader than the nucleus of *A. terricola*, two of the amoebae had nuclei with a length : breadth ratio of 4·2. In the other five, the L : B was between 1·5 and 1·9. Possibly the nucleus is somewhat compressed in one direction. The lengths of the nuclei were 38 to 72 μm, mean 51·4 μm. There are no elongate nucleolar bodies as in the typical *A. terricola*. Rather there are many small spherules, diameter about 1·5 μm, arranged in the outer region of the nucleus, with the greatest concentration toward the poles, so that the central part of the nucleus appears free of them. These spherules at the poles reach to the nuclear membrane, whereas in the typical *A. terricola* those poles are occupied by the elongate nucleolar bodies.
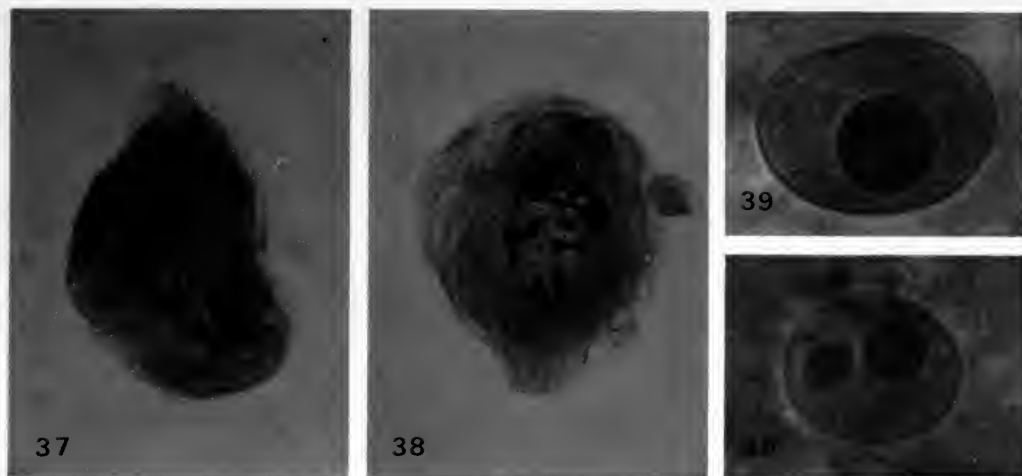
Figs 37–40 *Amoeba sphaeronucleolus* (= *Thecamoeba sphaeronucleolus*). (37), (38) Whole cells × 250. (39), (40) Nuclei × 1000. N = nucleus.

In some of these amoebae little or no ingested material was evident. In others the food vacuoles contained bacteria, one or two diatoms, fungal conidia, and possibly one or two protozoa and algal filaments.

The more hyaline appearance and apparently greater plasticity of these organisms compared with the typical *A. terricola* could be due partly to their not having ingested many food organisms for some time before observation and fixation. The somewhat greater size than Penard found for *A. terricola* might likewise be due to their form being less thick and compact because of the paucity of ingested material. The nuclear structure differs from that found in *A. terricola* by Penard and other workers. I am inclined to consider this a separate species, but examination of living material and possibly investigation of surface fine structure (Page & Blakey, 1979) is advisable.

Amoeba sphaeronucleolus Greeff, 1891
(Figs 37–40)

Penard, 1902, pages 121–125; 1905; 1913.

SLIDE NUMBER. 20.12.9.19.

TOTAL NUMBER OF AMOEBAE. 5.

DESCRIPTION AND REMARKS. The concept of this species which we follow today is that of Penard, and there is some uncertainty whether his *A. sphaeronucleolus* is that of the original author (Greeff, 1891; Page, 1977).

The form of Penard's specimens on this single slide agrees with the usual description of the species. The lengths of these five amoebae are 92 μm, 108 μm, 143 μm, 156 μm, and 161 μm, thus rather large by Penard's statements that he found large individuals to about 150 μm but they are often much smaller (Penard, 1902) and that in their maximum elongation they measure 100 to 130 μm (Penard, 1913). The nuclei are approximately spherical or ovoid. Four have a single, more or less spherical nucleolus, while the nucleolus of the fifth (Fig. 40) is in two large fragments accompanied by four smaller pieces which may also be nucleolar fragments. The largest dimensions of the five nuclei range from 22 to 30 μm. The nucleolus is quite smooth and more or less homogeneous except sometimes for a few small achromatic lacunae.

Ingested bodies include three diatoms and a conidium in one amoeba and apparent bacteria and algae in others.

These details correspond fairly well with those reported by workers since Penard, though the size of the nucleus and the texture of the nucleolus differ somewhat from those reported for a North American strain by Page (1977). Even given the more homogeneous nature of the nucleolus in Penard's preparations, this species is easily distinguished from *Thecamoeba quadrilineata* (Carter, 1856), which is a 'smooth' *Thecamoeba* rather than a 'rough' one (Page, 1977). There may be some variation amongst strains of *Thecamoeba* from different parts of the world, since the literature suggests variation even within Europe. However, investigators should be alert to the possible existence of more than one species of 'rough' *Thecamoeba* with a single compact central nucleolus or endosome.

Amoeba fibrillosa Greef, 1891
(Figs 41–45)

Penard, 1913; mentioned in Penard, 1902, pages 123, 124.

SLIDE NUMBERS. 20.12.8.7 (labelled *Amoeba alba* 'avec 1 *Amoeba fibrillosa*'); 20.12.8.8.

TOTAL NUMBER OF AMOEBAE. 5.

DESCRIPTION AND REMARKS. These multinucleate amoebae have the wrinkled pellicle and general form of a *Thecamoeba*, even though the form shows a greater variety and, even in the fixed preparations, evidence of a greater fluidity than that of the more typically *Thecamoeba*-like *Amoeba alba* (next section). In this respect it may be compared with *Thecamoeba proteoides* Page, 1976 (Page, 1976, 1977). Long, slender forms occur, sometimes with temporary branching (which can, however, occur occasionally even in the more rigid *A. alba*; see Fig. 46). Undoubtedly this temporary branching is associated only with a change of direction. Further comments on this character will be found in both Greeff (1891) and Penard (1913).

The largest of these amoebae is that on slide 20.12.8.7, shown in Fig. 41, which is 320 μm long though certainly not in the most extended form possible. The lengths of the other four are 228 μm, 228 μm, 226 μm, and 158 μm, this last one an irregular form. The length : breadth ratio of the larger amoeba in Fig. 43 is 4·1, ignoring the lateral pseudopodium near the posterior end, which was probably being withdrawn at the time of fixation. In Fig. 42, the pseudopodium with the hyaline cap (arrow) was undoubtedly the active one, with the other branch being withdrawn in a change of direction at the time of fixation.

In the large amoeba in Fig. 41, 97 nuclei were counted, and in another amoeba 85 could be found. Both these numbers undoubtedly err on the low side.

Although Penard (1913) said that the nuclei are 'normalement globuleux' though fairly often elongate, the elongated condition appears normal in these preparations (Fig. 44). Furthermore, observations while focussing suggest that many if not all the more spherical and ovoid forms (Fig. 45) are actually due to polar and oblique views of elongate nuclei. The single central nucleolus has in general the shape of the nucleus, though it often appears even more elongate (with long sides straighter) than does the nucleus. It is sometimes constricted in the middle to a dumbbell-like shape, which appears to be merely another variation and not a prelude to division as Penard (1913) thought.

The measurements of 25 nuclei in the largest amoeba ranged from 7·0 × 6·2 μm to 10·8 × 7·0 μm, with a mean greatest dimension of 8·9 μm.

A food vacuole in one amoeba contains an ingested organism which appears to be an amoeba, itself containing truncately bipyramidal crystals. Another amoeba also contains an ingested organism which appears to be a protozöon.

Greeff (1891) did not publish any illustrations of this species. (See remarks on *A. alba*.) Although I accept that this may well be the same species which Greeff saw, it must be pointed out that Greeff did not consider the nuclei to be elongate but described them as 'in der Regel rund, zuweilen leicht oval'. However, his description of the amoeba as a whole corresponds with this material. Since Greeff's description of *Amoeba fibrillosa* precedes in
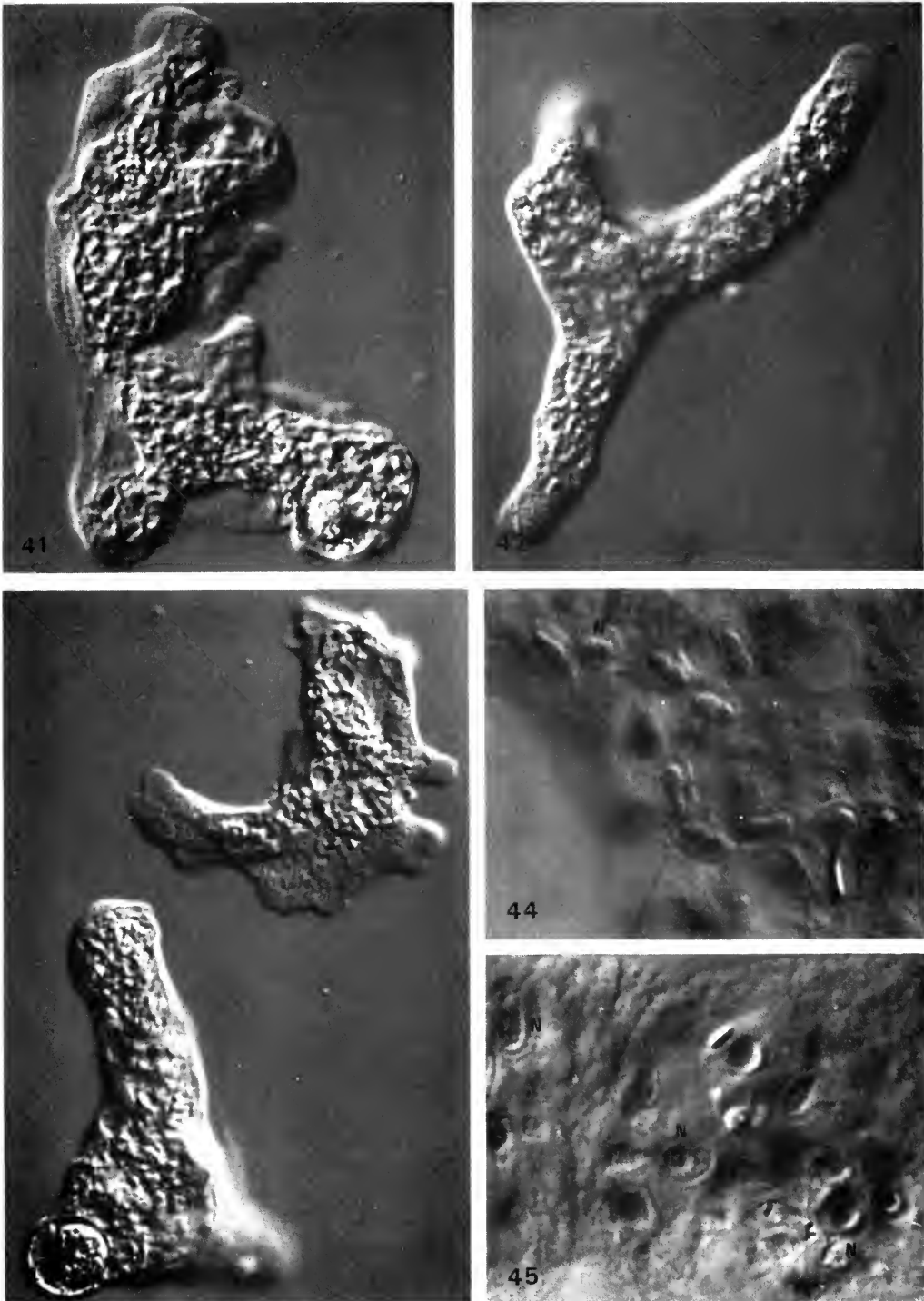
Figs 41–45 *Amoeba fibrillosa* (= *Thecochaos fibrillosum* comb. nov.). (41) to (43) Whole cells; arrow indicates hyaline cap on main pseudopodium in (42) × 250. (44), (45) Nuclei × 1000. N = nucleus.
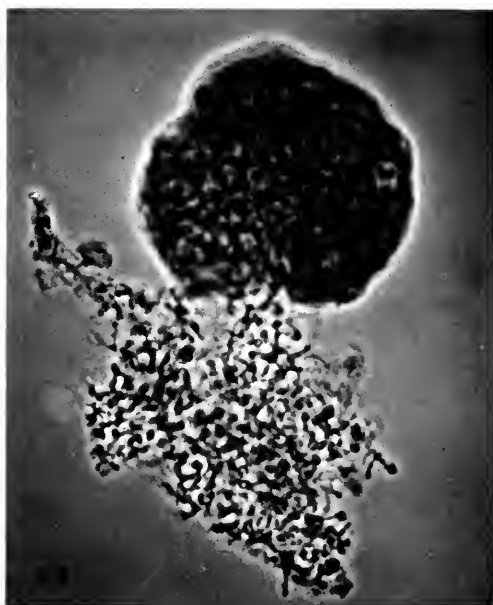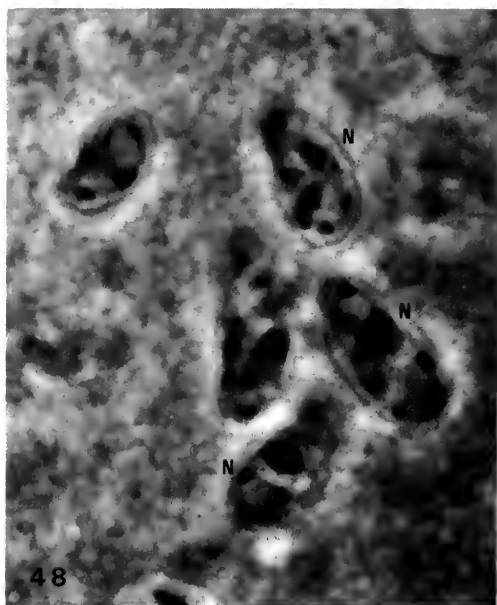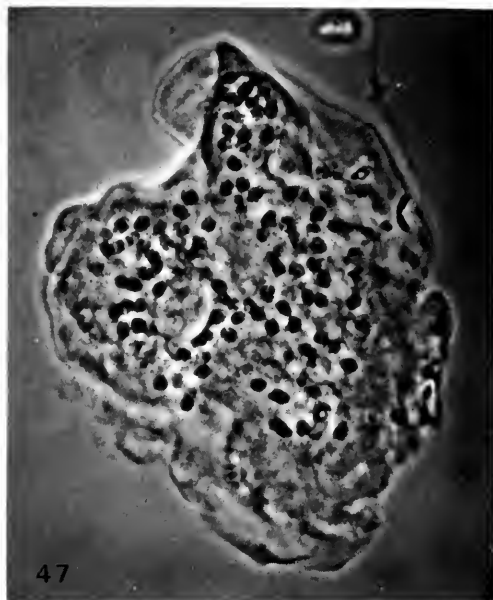
Figs 46–49 *Amoeba alba* (= *Thecochaos album* comb. nov.). (46), (47) Whole cells × 250. (48) Nuclei × 2000. (49) Amoeba apparently infected by fungus × 200.

the same publication his description of *A. alba* the former will be the type-species of the new genus being erected for the two. Penard, it will be noted, had more fixed material of *A. alba*, if this collection is representative.

Amoeba alba Greeff, 1891
(Figs 46–49)

Penard, 1902, pages 123–125; 1913.

SLIDE NUMBERS. 04.5.9.17; 20.12.8.1; 20.12.8.2; 20.12.8.3; 20.12.8.4; 20.12.8.5; 20.12.8.6; 20.12.8.7 ('avec 1 *Amoeba fibrillosa*').

TOTAL NUMBER OF AMOEBAE. 20.

DESCRIPTION AND REMARKS. This is another multinucleate species of Thecamoebidae, distinct in both locomotive form and nuclear structure from the preceding.

A number of these amoebae appear to have been in locomotion when fixed, thus representing the normal locomotive form well. Only the 15 amoebae which were apparently fixed before they died of bursting or other causes than fixation were measured. Their lengths were 166 to 276 μm, with a mean of 210 μm; their length : breadth ratios were 1·1 to 2·2, with a mean of 1·4, quite normal proportions for a *Thecamoeba*.

Use of an oil immersion objective and phase contrast optics permitted a closer look at the nuclei than Penard could have and resulted in a more accurate picture of their structure. However, the same problems which Penard encountered remained in counting the nuclei because, as he said, 'la plupart ne deviennent visibles qu'après compression de l'Amibe' (Penard, 1902), and compression was, of course, impossible. Attempts to count the nuclei in five favourable specimens yielded results of 94, 100, 102, 145, and 185, in each case certainly below the actual number. In 1902 Penard thought that the number might reach several hundreds, but in 1913 he said only that it often exceeded 100.

The nuclei (Fig. 48) appeared more ovoid/ellipsoid, i.e., more elongate, in some amoebae, and more spherical to ovoid, i.e., less elongate, in others. The more elongate nuclei, 25 from each of the two amoebae, measured from 7·0 × 5·6 μm to 12·0 × 5·6 μm, with a mean of 9·0 μm for the greatest diameter. The more spherical nuclei, 25 from one amoeba, had a greatest diameter of 6·5 to 7·5 μm, with a mean of 7·0 μm. The presumed nucleolar material was not scattered as spherules through the nucleus, as described by Penard (1913) ('disséminés . . . dans un suc nucléaire') and shown in Fig. 2, page 123, of Penard (1902) and Fig. 7 of Penard (1913). Rather, it was arranged parietally as variously shaped bodies, some band-shaped, which may all have been lobes of one or two parietal bands in each nucleus. These photomicrographs were made with an oil-immersion lens and phase-contrast optics, not available to Penard.

Ingested material included apparent algal filaments and a few diatoms. One slide (20.12.8.6) bears the notation 'Parasitée par cryptogame'. This preparation (Fig. 49) contains a more or less rounded amoeba with a mass of branching, non-septate filaments coming out of an invagination. The diameter of these filaments is about 2 μm or slightly more. Penard presumably examined this amoeba alive before fixing it; otherwise one might question whether the filaments were parasitizing the amoeba or the amoeba ingesting the filaments.

With his original description of *A. alba*, Greeff (1891) published no illustrations, an omission which led Page (1977) to doubt whether Greeff's organism was indeed a *Thecamoeba* and speculate whether it might not be a *Leptomyxa*, a fairly common genus of multinucleate amoebae in soil. However, Penard (1902) agreed with Greeff that *A. alba* is very rare. I have myself never seen a multinucleate *Thecamoeba*-like organism in many collections from nature and do not know of any reports of them by workers other than Greeff, Penard, and Cash & Wailes (1919). The figure published by Cash & Wailes is not very informative, but their text suggests that they may have had the same species as Penard. They also described *A. alba* as rare. A consideration of Greeff's description in the light of the Penard slides makes it quite likely that Penard's organism is the same as Greeff's.

Amoeba granulosa Gruber, 1885
(Fig. 50)

Penard, 1902, pages 46–48.

SLIDE NUMBER. 06.4.27.2.

TOTAL NUMBER OF AMOEBAE. 1.
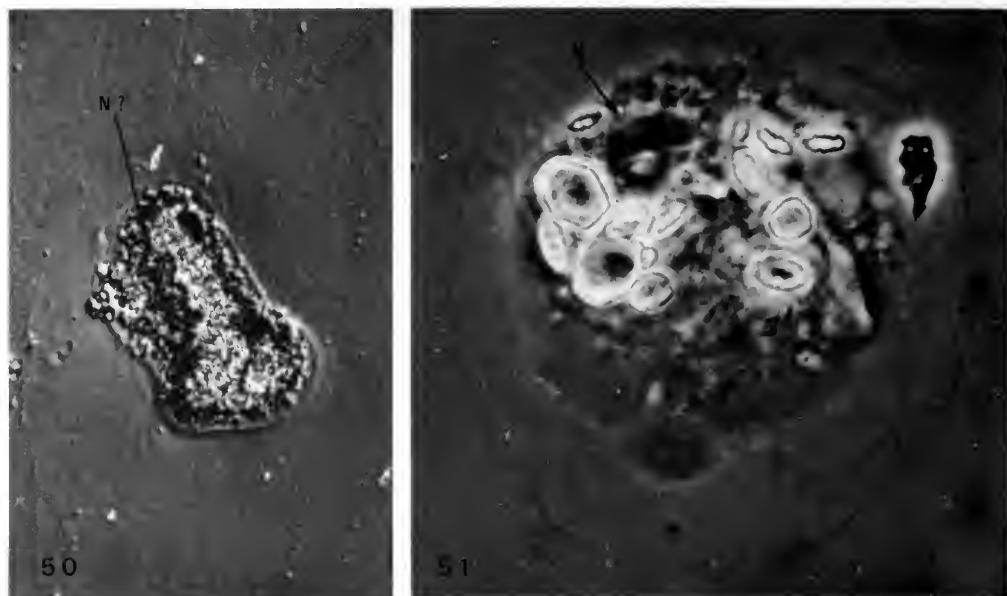
Fig. 50 *Amoeba granulosa* × 250. N? = location of possible nucleus.

Fig. 51 *Amoeba lucens* (= *Saccamoeba lucens*), not normal locomotive form. × 800. N = nucleus.

DESCRIPTION AND REMARKS. The single amoeba of this species which Penard said that he found in great abundance furnishes little information. Because of the thickness of the mount, it could be examined only with the × 10 objective. At any rate, the amoeba does not appear well preserved. It is flattened but not circular in outline so presumably not dead or moribund when fixed. Inside the narrow hyaloplasmic border which occupies most of the periphery, the cytoplasm is filled with formed elements, somewhat less densely packed in the central region of the cell. These elements appear to be bipyramidal crystals, as Penard thought. A slightly stained area which may be the nucleus is indicated in Fig. 50 by an arrow. The dimensions of the cell are $142 \times 88 \ \mu$m; the diameter of the possible nucleus is about 29 μm.

Although this looks like the flattened cells figured by Gruber (1885), the identification is questionable. Gruber gave the diameter as 'ungefähr 0·03 mm', which Penard (1902) mistranslated as 'de 300μ'. Their descriptions of the nucleus do not appear to agree, although the apparent difference may be due to either optics or terminology.

At any rate, one would not like to hazard a guess on the identity of this amoeba, though an amoeba with such an abundance of crystals (undoubtedly not silica, agreeing with Penard rather than Gruber) might be recognizable if found again. It might be mentioned that in this paper Gruber (1885) deplored the impossibility of identifying an amoeba with any degree of certainty.

Amoeba lucens (Frenzel, 1892)
(Fig. 51)

Penard, 1902, pages 55–57.

SLIDE NUMBER. 04.5.9.18.

TOTAL NUMBER OF AMOEBAE. 1.

DESCRIPTION AND REMARKS. Although Penard (1902) illustrated his description of this species with a drawing (Fig. 1, page 56) of what is obviously a *Saccamoeba*, the single cell on this slide is not so unambiguous. In fact, it might be taken for a *Cochliopodium* with scales
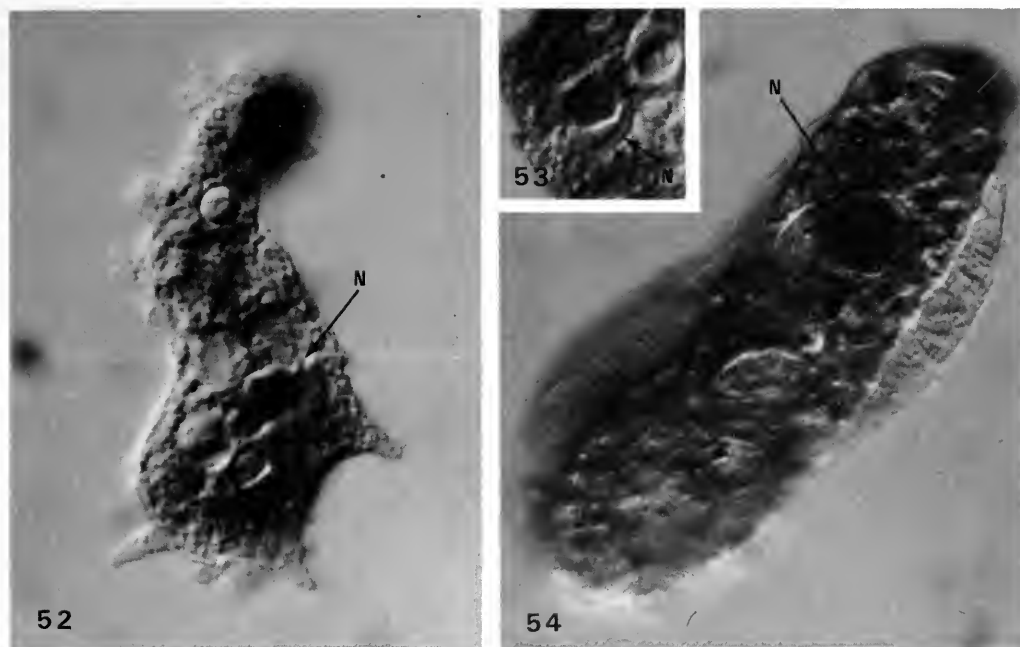
Figs 52, 53 *Amoeba vespertilio* (= *Mayorella vespertilio*); both figures of same cell, focussed on pseudopodia in (52) and on nucleus in (53) × 1000. N = nucleus.

Fig. 54 Unidentified amoeba on same slide with *A. vespertilio* × 800. N = nucleus.

either lost or invisible to the light microscope, if it were not for Penard's label. This cell appears to be made up of a more or less discoid granular mass surrounded by a flattened hyaline border of varying width. The diameter of the granular region is $72 \times 65 \, \mu$m; including the hyaline border the cell is $90 \times 73 \, \mu$m. The most striking feature is, of course, the truncately bipyramidal crystals, of which there are about a dozen, the largest approximately $13 \times 10 \, \mu$m. Some crystals are slightly deteriorated. The nucleus seems poorly fixed, but using Penard's description as a guide, this appears to be a nucleus in which the diameter of the central nucleolus is only a little less than that of the nucleus. The dark area which appears to be the nucleolus has a maximum diameter about $15 \, \mu$m. Although the nuclear membrane (usually quite distinct in *Saccamoeba*) is not preserved, the narrow clear halo around the nucleolus suggests a maximum nuclear diameter of 19 to $20 \, \mu$m. The amoeba appears to contain at least one fungal conidium.

Despite the puzzling form of this preserved amoeba, Penard's account leaves no doubt of its identity, though this slide is of value chiefly for the structure of the crystals and, to a lesser degree, that of the nucleus. *Saccamoeba lucens* has been re-described by Bovee (1972) and is recognized as the type-species of the genus *Saccamoeba*. There is some inconsistency among the descriptions of Frenzel (1892), Penard, and Bovee (1972).

Amoeba vespertilio Penard, 1902
(Figs 52–54)

SLIDE NUMBER. 20.12.8.29.

TOTAL NUMBER OF AMOEBAE. 1 of this species.

DESCRIPTION AND REMARKS. Only one of the two organisms on this slide can belong to this species or even to the genus *Mayorella* Schaeffer, 1926, in which *Amoeba vespertilio* is now classified. The other (Fig. 54) is elongate, apparently with flattened hyaline borders along the sides and with a different nuclear structure.
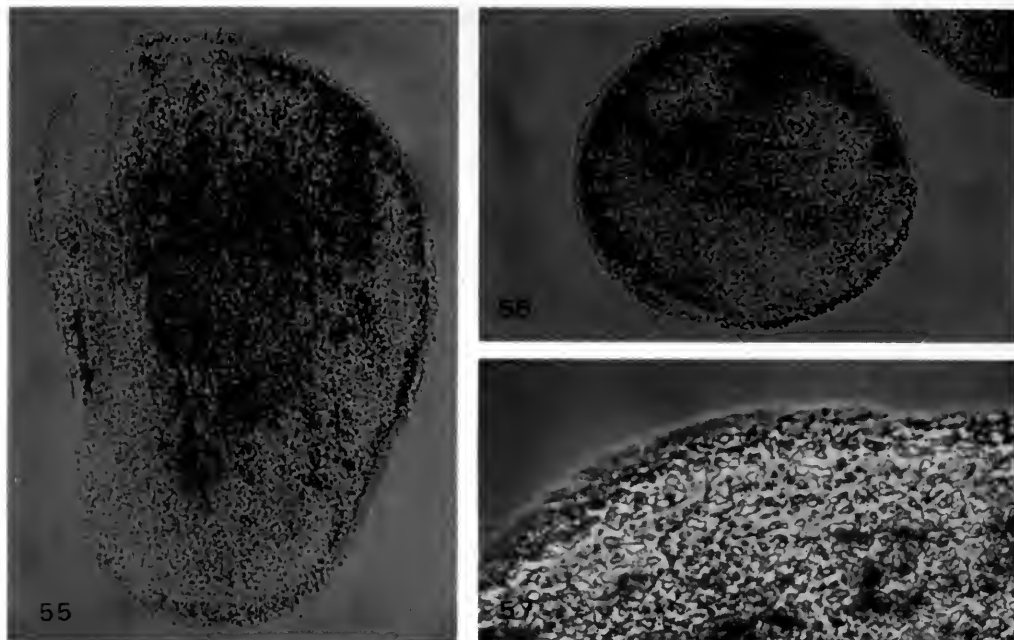
Figs 55–57   *Amoeba muralis.* (55), (56) Whole cells × 80. (57) Edge of cell, enlarged to show mineral grains × 250.

The amoeba which can be identified as *A. vespertilio* is 65 μm long × 31 μm wide, not including the conical pseudopodia, of which there are six or seven, counting those which have been relegated to the sides. These pseudopodia (Fig. 52), in their fixed and probably somewhat shrunken condition, are up to 9 μm long, with a basal diameter of about 4 μm. The appearance of the uroid (posterior end) suggests that as the amoeba advances the conical pseudopodia, after passing to the posterior end, form a small clump of blunt projections at the uroid before being resorbed. The nucleus (Fig. 53) has a diameter of 12·5 μm and the central nucleolus a diameter of 7·7 μm. The amoeba contains at least one ingested algal cell.

Despite the shrinkage accompanying fixation, this amoeba represents the typical *Mayorella* form much better than do the illustrations on page 94 in Penard (1902). It most resembles, among more recently described species, *Mayorella oclawaha* Bovee, 1970, and *M. riparia* Page, 1972, though both the amoeba and the nucleus are larger than the sizes reported for those species (Page, 1976). It would not be safe to derive a specific diagnosis from this single cell, since it is not possible even to know whether its length is large, small, or average for the species.

<center>

Amoeba muralis Penard, 1909
(Figs 55–57)

</center>

Slide number. 20.12.8.11.

Total number of amoebae. 11.

Description and remarks. Because Penard (1909*a*) considered this a naked amoeba rather than one with a flexible test and accordingly placed it into the genus *Amoeba*, it is included in this study.

This preparation contains eleven very flattened, mostly circular cells arranged in a ring. Four appear to have disintegrated, with their positions now marked chiefly by the foreign material which had covered their surfaces, though the outlines are still distinct enough for measurements of diameter. The thickness of the preparation did not permit use of an

objective above × 10, but it is doubtful that a higher magnification would have yielded more information. All the amoebae were covered with foreign matter, apparently mineral grains with a maximum dimension of 5 to 10 μm. There are in some cells patches of denser material, probably internal and possibly the remains of ingested algal or other plant matter. The edge of the cell (or its endogenous covering) appears as a clear border extending 5 or 10 μm beyond the mineral grains around much of the periphery of some cells, with some extraneous particles helping to mark its outer edge. I could not find any nuclei, of which Penard said there might be 40, 50, or 60.

These cells are marked by multiple parallel streaks, as if scraped during preparation.

Penard (1909a) described this as a multinucleate amoeba which could secrete a mucilaginous envelope. According to him, this envelope kept particulate matter at a distance from the cell surface. However, when the amoeba began locomotion, the mucilage disappeared, first in the anterior region, then finally from the entire surface.

One genus of amoebae with a flexible test which can be detected only with difficulty is *Gocevia* Valkanov, 1932. The description given by Penard suggests that *A. muralis* may be covered by a cuticle which may accumulate foreign matter and which may stretch and become thinner during locomotion. His description of fine, digitiform pseudopodia also recalls some recently investigated organisms classified in that genus. The characters of *Gocevia* with descriptions of organisms which appear to belong to that genus are discussed most recently by Page & Willumsen (1980). *Gocevia* belongs to the family Cochliopodiidae, in the Testacealobosia. However, all known members of the genus are normally uninucleate except one which may be normally binucleate.

Dinamoeba mirabilis Leidy, 1874
(Fig 58, 59)

Penard, 1902, pages 134–137; 1909b; 1936.

Slide number. 04.5.9.154.

Total number of amoebae. 1.

Description and remarks. This amoeba shows some signs of shrinkage in fixation in that some of the conical pseudopodia appear shrunken in diameter, though the hyaline pseudopodia of this genus are at any rate quite fine even in life (Fig. 59A, Page, 1976). The cell is 94 μm long, with a maximum breadth of 37 μm, neither measurement including the pseudopodia. On either side of the anterior end, which appears to have a shallow hyaline cap, is one pseudopodium, with lengths of 15·5 and 19 μm. There are several single pseudopodia along the sides, as well as one broad, flat, hyaline projection bearing three short pseudopodium-like extensions. At the posterior end are several uroidal filaments which appear to have originated by adhesion to the substratum but could be pseudopodial remnants.

Although Penard (1902, 1909b) emphasized that the organisms which he saw were as a rule binucleate, this cell contains only one nucleus, situated toward the posterior narrowed 'neck' and elongated by cytoplasmic movement. The diameters of the nucleus are 20 × 9 μm; of the compact central nucleolus, about 8·5 × 6·2 μm.

The cytoplasmic pigmentation, including granules, suggests an algal diet, and two or three ingested cells are distinguishable.

I could not make out any of the bacterium-like objects, adherent to the surface, which are characteristic of many reported *Dinamoeba*, though they may also be absent from living amoebae (see Fig. 59A, Page, 1976).

The possible identity of *D. mirabilis* with *Mastigamoeba aspera* Schulze, 1875, has been discussed by Penard (1909b, 1936), De Groot (1936), and Page (1970). This slide sheds no further light on that question.
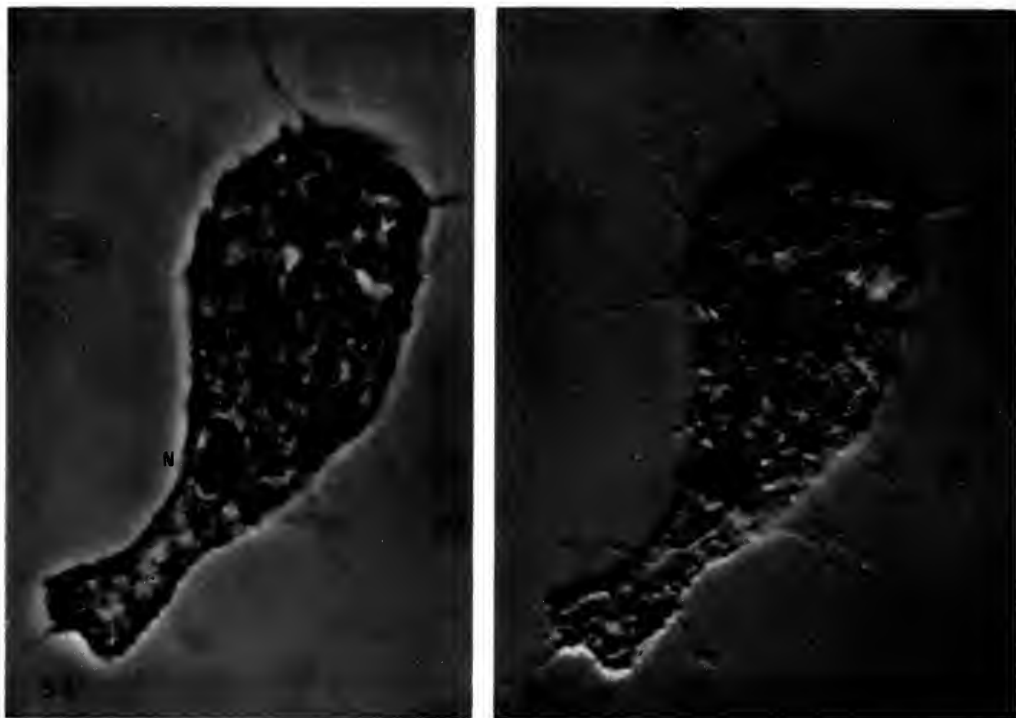
Figs 58, 59   *Dinamoeba mirabilis*, both of same cell × 800. (58) Phase contrast, to show nucleus distinctly. (59) Differential interference contrast, to show pseudopodia distinctly. N = nucleus.

Pelomyxa palustris Greeff, 1874
(Figs 60, 61)

Penard, 1893; 1902, pages 138–143.

SLIDE NUMBERS. 04.5.9.206; 04.5.9.210; 06.4.27.7; 20.12.8.530; 20.12.8.531; 20.12.8.532; 20.12.8.533.

TOTAL NUMBER OF AMOEBAE. 16.

DESCRIPTION AND REMARKS. These are recognizable as the species universally designated by this name. Some of the cells are more or less rounded, others an elongated ovoid, i.e., the usual locomotive form. The longest reached 1478 μm; two 'jeunes individus' are 175 and 233 μm long. In some the mineral grains are so abundant as to hinder observations of other inclusions; some mineral grains measure more than 50 μm, but most are much smaller. Nuclei are numerous. A total of 125 nuclei, 25 in each of five amoebae, had diameters from 7·0 to 14·5 μm, with a mean of 9·2 μm; only in one of these five amoebae did the diameters exceed 10·8 μm, however. Some of the nuclei (Fig. 61) had a rather shrivelled appearance. In the nuclei there was usually a parietal layer of small granules, sometimes a few larger, darkly staining pieces of various shapes and sizes just beneath the nuclear membrane, sometimes a small body that appeared to be near the centre of the nucleus, and often some rather indistinct filamentous material. The amoebae often contained many diatoms, occasionally filamentous ones. Rods that appeared to be the characteristic symbiotic bacteria were up to 5 μm long. The cytoplasm was often highly alveolar.

   Since there is no question about the identity of these amoebae and since the characters of the species are well known today, only two of the photomicrographs are reproduced here.
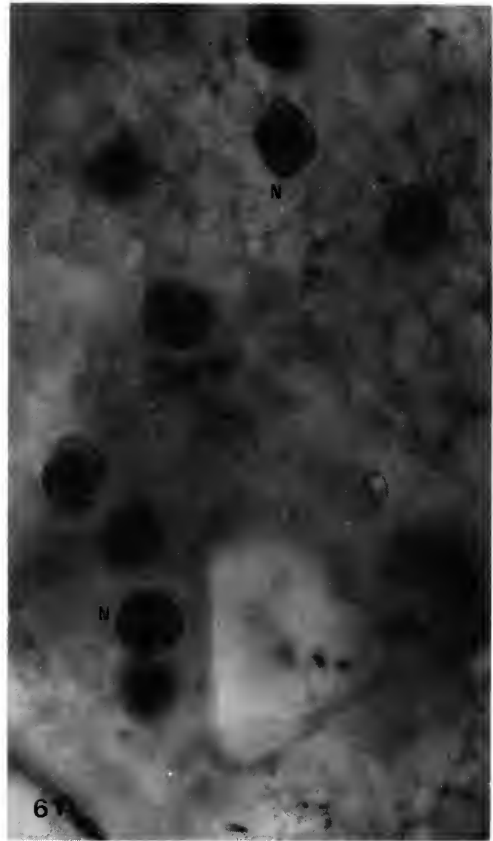
Figs 60, 61 *Pelomyxa palustris*. (60) Whole cell, with anterior end at top × 100. (61) Nuclei × 1000. N = nucleus.

Pelomyxa fragilis Penard, 1904
(Figs 62–65)

SLIDE NUMBERS. 04.5.9.209, 20.12.8.529.

TOTAL NUMBER OF AMOEBAE. 4.

DESCRIPTION AND REMARKS. Since the amoeba on slide 04.5.9.209 was so obscured by detritus that few useful observations could be made, this description is based entirely on the three amoebae on slide 20.12.8.529.

Although these amoebae certainly appear more changeable in form than the typical *Pelomyxa palustris*, none has pseudopodia which can be described, in Penard's term, as '*déchiquetés*', presumably referring to the form in Fig. 2 of Penard (1904). They do have secondary lateral pseudopodia, probably being retracted in a change of direction at the time of fixation. Shallow, crescent-shaped hyaline caps are distinguishable on two amoebae (Figs 62, 64). The uroidal regions of two (Figs 63, 64) appear somewhat drawn out as if by adhesion. The lengths and length : breadth ratios (not including lateral pseudopodia) are: 398 μm, L : B 3·0; 403 μm, L : B 3·6; and 456 μm, L : B 4·3.

These amoebae appear to contain hundreds of nuclei each; in one, there were at least 175 to 200. The diameters of the nuclei, 25 measured in each of the three cells, ranged from 5·4 to 7·7 μm, with a mean of 6·5 μm. The nuclei (Fig. 65) had a ring of darkly staining material just beneath the nuclear membrane and a roughly spherical or ovoid inner body which might
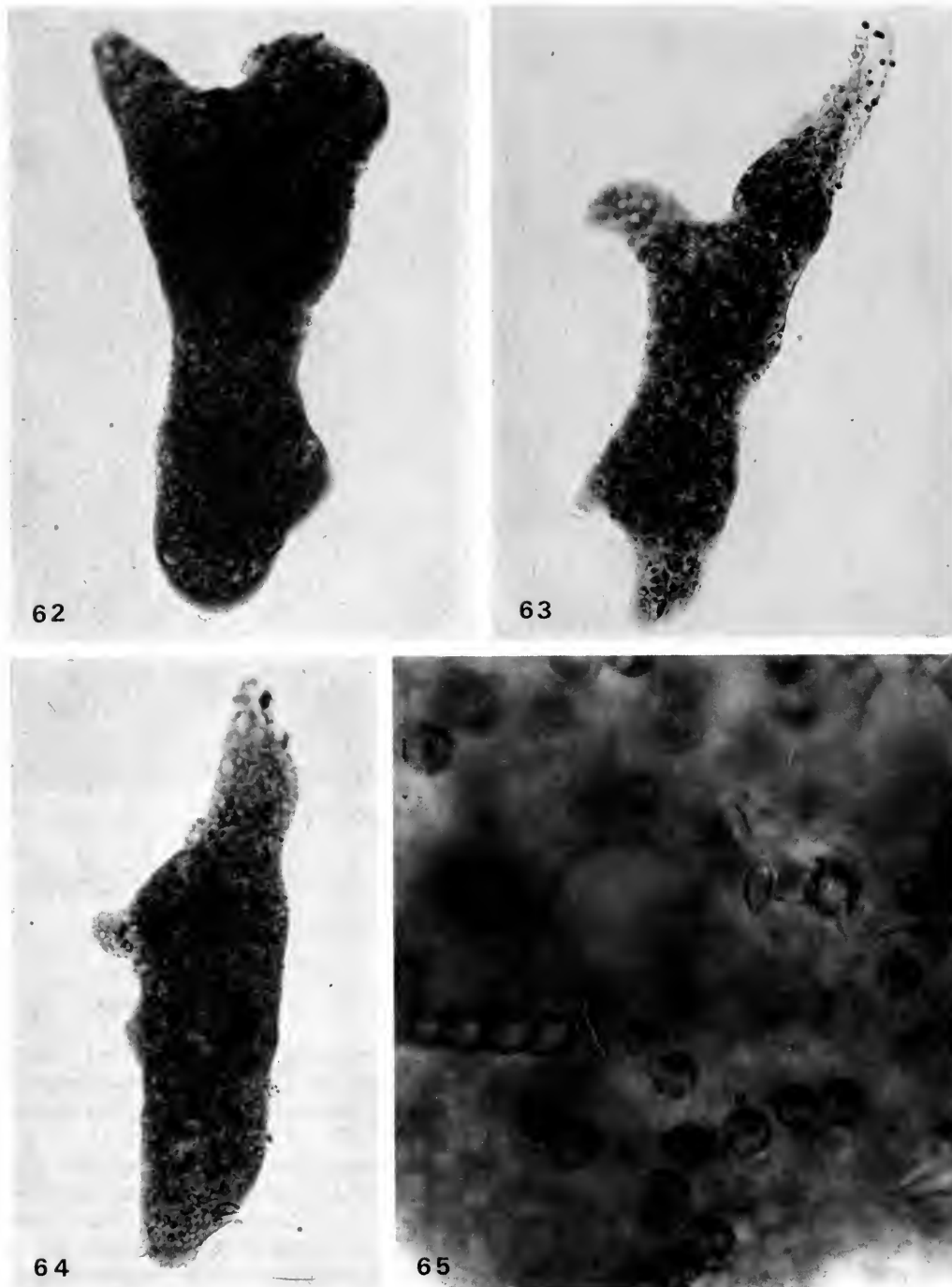
Figs 62–65 *Pelomyxa fragilis.* (62) to (64) Whole cells × 200. (65) Nuclei × 1000. N = nucleus.

be central or eccentric; sometimes there appeared to be two of these presumed nucleoli (see Penard, 1904).

Ingested material included many diatoms, other unicellular algae, a few short algal filaments, and, in one amoeba, possibly a *Colpoda*. I could not identify any mineral grains
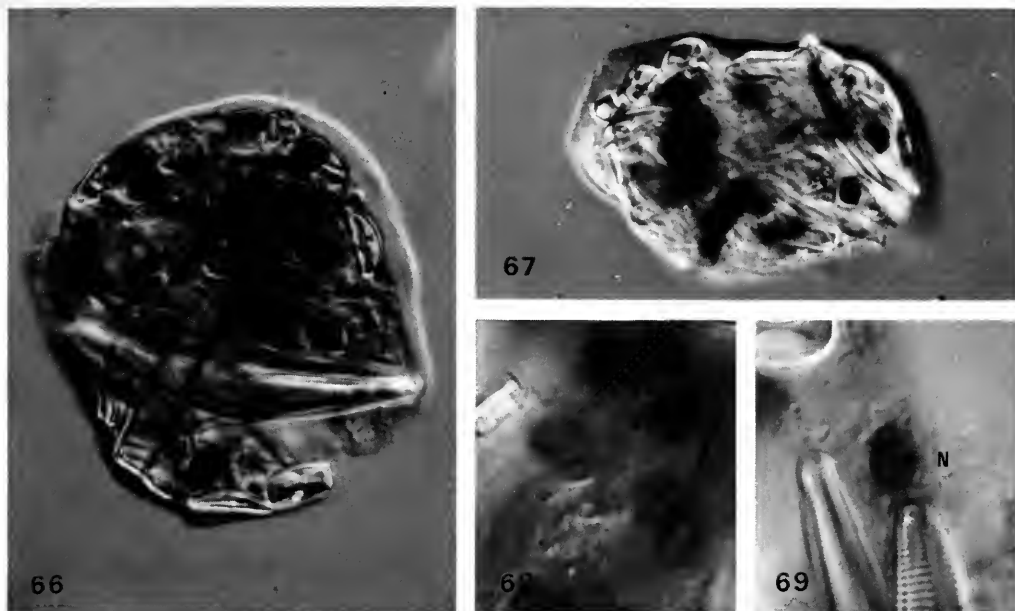
Fig 66–69 *Pelomyxa vivipara*. (66), (67) Whole cells × 250. (68), (69) Nuclei × 1000. N = nucleus.

with certainty within the amoebae, although a few possible mineral particles (or glass fragments?) appeared to be adherent to the outer surfaces. Nor could I identify with certainty the symbiotic bacteria, which Penard reported to be abundant. The cytoplasm appeared highly alveolar.

Accepting the presence of symbiotic bacteria, these amoebae differ from the typical *Pelomyxa palustris*, as far as can be determined from these fixed individuals, chiefly in their greater deformability and almost certainly greater pseudopodial activity, and in the absence of ingested mineral particles. It may be that their greater motility is, in fact, due to their not being packed with those particles. The difference in nuclear structure may not be of major importance, considering the variations reported for *P. palustris* (Daniels & Breyer, 1967; Andresen, Chapman-Andresen & Nilsson, 1968).

P. fragilis may therefore well be a synonym of *P. palustris*.

Pelomyxa vivipara Penard, 1902
(Figs 66–69)

SLIDE NUMBER. 20.12.8.534.

TOTAL NUMBER OF AMOEBAE. 2.

DESCRIPTION AND REMARKS. These two cells look like sacs packed with diatoms. Their measurements are $211 \times 182 \mu m$ and $187 \times 127 \mu m$, and each is approximately 70–$80 \mu m$ thick. Along part of the periphery of each cell is a narrow hyaline zone (extending inward up to $12 \mu m$ from the edge). Both are full of diatoms, and in one at least one desmid was seen. No mineral grains are present in either. Useful observations of the nuclei were possible in only one of the two amoebae, which contained well over 60 nuclei. The nuclei (Figs 68, 69) are circular to oval in outline, and much of the stained granular material is parietal in each nucleus. The diameters of 25 nuclei ranged from 7.7 to $9.2 \mu m$, with a mean of $8.6 \mu m$. Bacteria-like rods were discernible in the cytoplasm, particularly near the nuclei, as reported by Penard.

Penard described and figured 'embryos' in these amoebae, i.e., small amoebae, which

might have been parasites or might have been ingested cells which were extruded before digestion. No information on that phenomenon could be gained from this preparation.

Modern workers would tend to regard these amoebae as another phase of *P. palustris* lacking mineral grains, a matter to which reference will be made in connection with the next two species.

Pelomyxa belevskii Penard, 1893
(Figs 70–74)

Penard, 1893; Penard, 1902, pages 144–146.

SLIDE NUMBER. 04.5.9.207.

TOTAL NUMBER OF AMOEBAE. 1.

DESCRIPTION AND REMARKS. This single cell measures $470 \times 398 \, \mu m$ and appears considerably compressed. The first thing which strikes the eye is the ingested plant matter, all apparently derived from vascular plants, which Penard (1902) identified as decaying leaf fragments. The cell membrane is somewhat wrinkled around much of the periphery. Focussing carefully, one can find at some places on the cell fine projections, sometimes sharply pointed and single, at other times broader, irregular, and somewhat divided, if indeed these two kinds of projections are the same thing, as Penard thought (Figs. 72, 73). At one point there is also a broad, flat lobe bearing many fine projections (Fig. 71). On this preserved cell, the projections showed up best with differential interference contrast, and one must wonder at Penard's visual acuity that he could make them out with his optical system.

This amoeba contained no mineral grains, and the presence of symbiotic bacteria was not confirmed, though one must accept Penard's report of their presence. Twelve nuclei (Fig. 74) were seen, with finely granular material forming a layer against the inner surface of the nuclear membrane, though an area to one side of a nucleus might appear free of it, perhaps as the result of shrinkage during fixation. The nuclear diameters were strikingly greater than in the preceding three species of *Pelomyxa,* ranging from 24 to 29 μm, with a mean of 26 μm.

The fact that some of the tiny projections from the surface (*aiguillons* or *aspérités*) are very fine suggests the possibility that these are actually non-motile flagella of the type reported by Griffin (1972, 1979) for *P. palustris*, but the broad lobe in Fig. 71 has the appearance of an adhesion uroid with pseudovilli, and one cannot be certain that at least some of the other projections are not such pseudovilli, though the single ones look somewhat more like flagella.

P. belevskii is one of the named species which Chapman-Andresen (1978) has suggested may be a phase of *P. palustris*.

Pelomyxa binucleata (Gruber, 1885)
(Figs 75–81)

Penard, 1902, pages 147, 148.

SLIDE NUMBERS. 04.5.9.208; 20.12.8.528.

TOTAL NUMBER OF AMOEBAE. 13.

DESCRIPTION AND REMARKS. These amoebae are generally ovoid to ellipsoid, usually so packed with algae as to resemble sacs pushed out here and there by the ends of filaments. None of the uroidal villi pictured by Penard could be seen in the fixed preparations, although the posterior end is sometimes a little morulate or shrivelled. The lengths were from 96 to 240 μm, with a mean of 159 μm; length : breadth ratios 1·0–1·9, mean 1·4. Some of the many contained algal filaments are bent, but none appear to be reflected back upon themselves. Some amoebae also contain diatoms and other unicellular algae. Apparent symbiotic
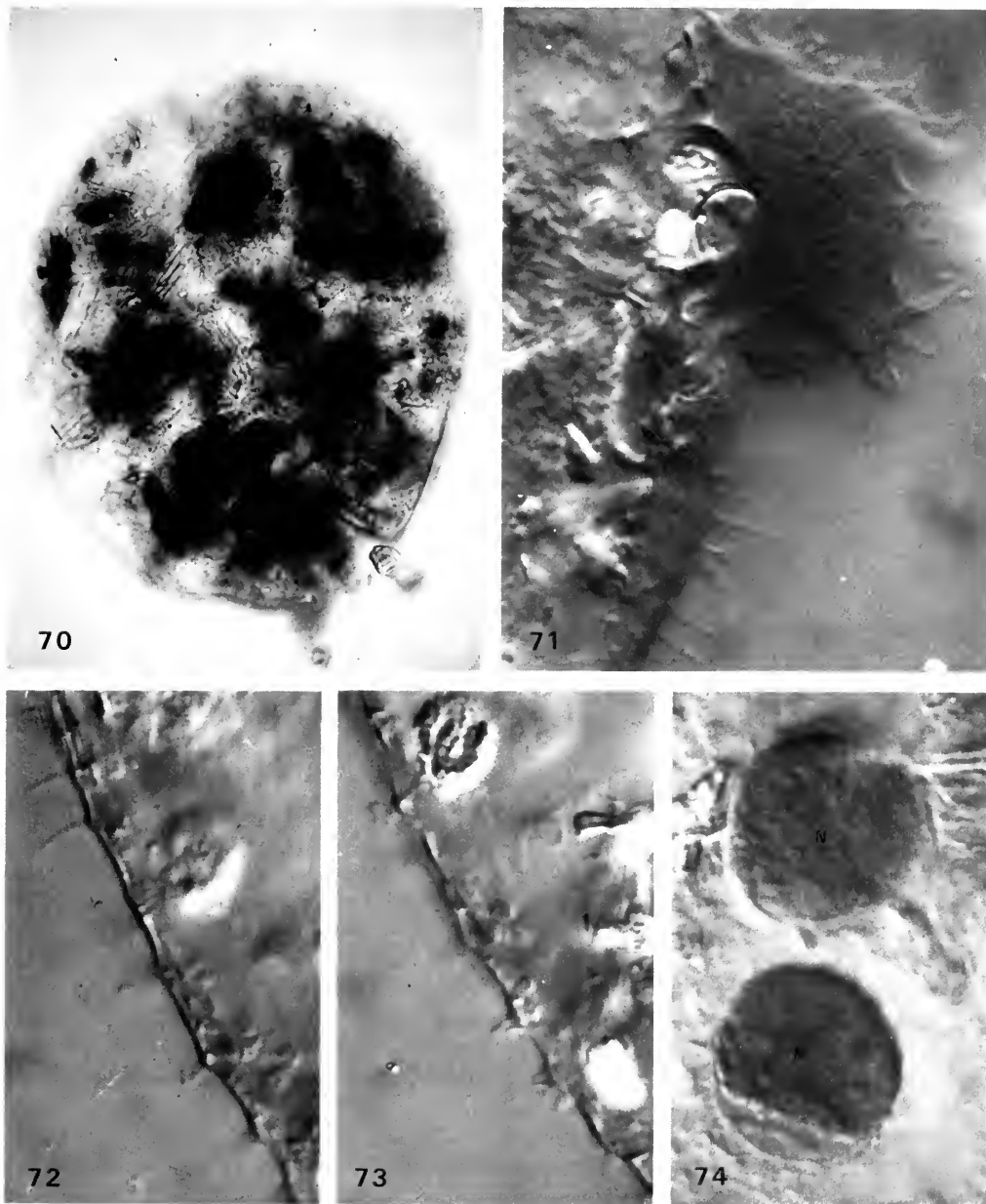
Figs 70–74 *Pelomyxa belevskii.* (70) Whole cell, showing ingested remains of vascular plants and several nuclei, two of which are in focus at right of picture × 150. (71) Fine projections on both broad lobe (upper right of picture) and main cell body × 1000. (72), (73) Single and more complex projections from cell surface × 1000. (74) Two nuclei × 1000. N = nucleus.

bacteria could be distinguished with differential interference contrast. No mineral grains were identified with certainty.

All the amoebae are binucleate, with the two nuclei fairly close together in some cells but widely separated in others. Generally the diameters of the two nuclei in a given cell are similar, and the differences are slight enough to be accounted for by angle of viewing. The 26 nuclei had maximum diameters ranging from 19 to 34 μm, with a mean of 24·3 μm. Some nuclei were isodiametric, but in others the two diameters measured differed slightly. The
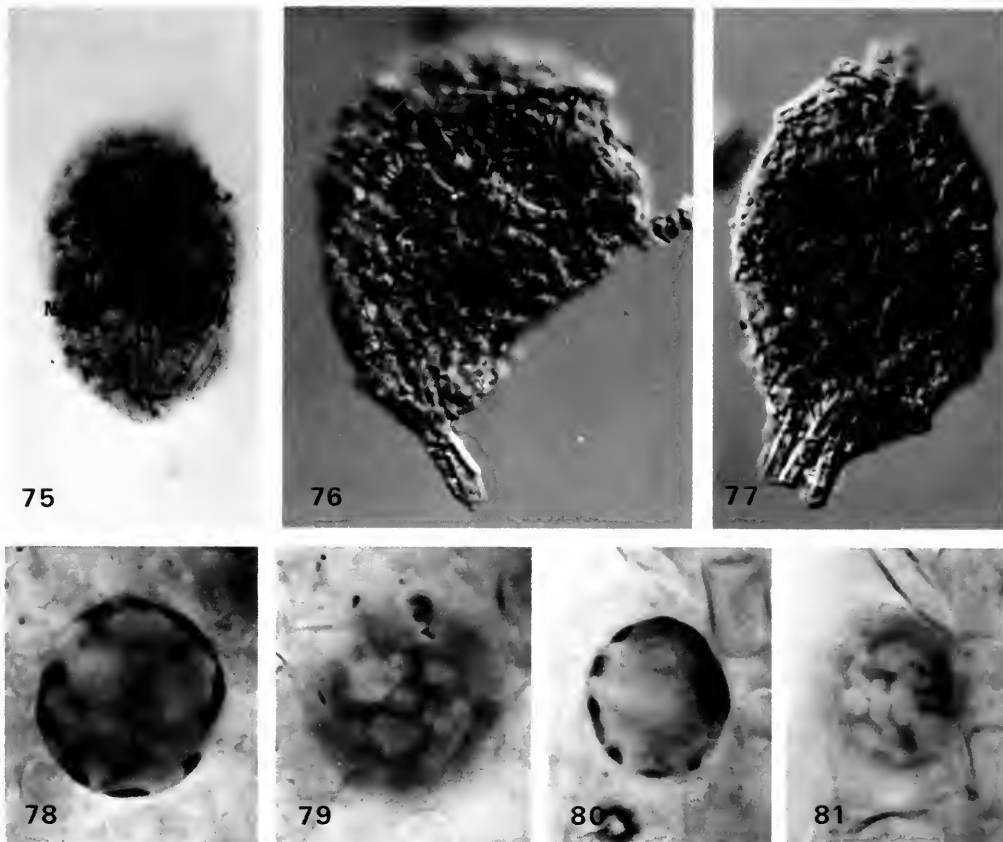
Figs 75–81   *Pelomyxa binucleata.* (75) Whole cell showing both nuclei × 250. (76), (77) Cells distorted by ingested algal filaments × 250. (78), (79) Same nucleus at different levels to show both parietal arrangement and reticulate form of nucleolar material × 1000. (80), (81) Another nucleus at two levels to show nucleolar structure × 1000. N = nucleus.

presumed nucleolar material was generally parietal, sometimes appearing to exist as fragmented bodies, sometimes as granules or larger clumps. However, in the best-preserved nuclei, what appeared to be small nucleolar pieces in one optical plane could be seen on focussing into another plane to be part of a reticulum just inside the nucleus, as shown in Figs. 78–81.

Again, one cannot say definitely whether *P. binucleata* is a distinct species or fits into the cycle of phenotypic change in *P. palustris* (Chapman-Andresen, 1978). The nuclei appear distinctive, but one could explain the absence of mineral grains associated with a shape differing from that of *P. palustris* as a stage on the way to maturation.

Generic diagnosis

Phylum **SARCOMASTIGOPHORA**
Subphylum **SARCODINA**
Superclass **RHIZOPODA**
Class **LOBOSEA**
Subclass **GYMNAMOEBIA**
Order **AMOEBIDA**
Family **THECAMOEBIDAE**

Genus *THECOCHAOS* nov.

DERIVATION OF NAME. From *Theco-* + *Chaos* because *Thecochaos* (multinucleate) bears a relationship to *Thecamoeba* (uninucleate) in the family Thecamoebidae similar to that of *Chaos* (multinucleate) to *Amoeba* (uninucleate) in the family Amoebidae.

DIAGNOSIS. Broad, flattened, often irregularly oval to oblong in outline but sometimes more elongate, always with length greater than breadth in locomotion, with surface folds and wrinkles and light-microscopical appearance of a thickened pellicle; hyaloplasm a more or less crescentic cap at anterior end, sometimes with slender lateral extensions; branching usually only when changing direction; multinucleate. Essentially a multinucleate *Thecamoeba*.

TYPE-SPECIES. *Thecochaos fibrillosum* (Greeff, 1891).

Classification

Subclass GYMNAMOEBIA
  Order AMOEBIDA
    Family AMOEBIDAE
      Amoeba proteus Leidy, 1878 (including *A. nitida*, junior synonym)
      Amoeba sp.
      Chaos nobile (Penard, 1902) comb. nov.

    Family THECAMOEBIDAE
      Thecamoeba terricola (Greeff, 1866)
      Thecamoeba papyracea (Penard, 1905) comb. nov.
      Thecamoeba sphaeronucleolus (Greeff, 1891)
      Thecochaos fibrillosum (Greeff, 1891) comb. nov.
      Thecochaos album (Greeff, 1891) comb. nov.

    Family HARTMANNELLIDAE
      Saccamoeba lucens Frenzel, 1892

    Family PARAMOEBIDAE
      Mayorella vespertilio (Penard, 1902)
      (*Dinamoeba mirabilis* Leidy, 1874?)

  Order PELOBIONTIDA
    Family PELOMYXIDAE
      Pelomyxa palustris Greeff, 1874
      (Validity of other species of *Pelomyxa* questionable.)

Incertae sedis: *Amoeba granulosa*, *Amoeba laureata*, *Amoeba muralis*, '*Amoeba peritissima*' (nomen nudum).

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British Museum (Natural History)

An Atlas of Freshwater Testate Amoebae

C. G. Ogden & R. H. Hedley

1980, Hardcovers, 222pp, £17.50 (£18.00 by post). Co-published by British Museum (Natural History) and Oxford University Press.

This book illustrates, using scanning electron micrographs, most of the common species of testate amoebae that are found in freshwater habitats. Information on the biology, ecology, geographical distribution and a classification are followed by descriptions of ninety-five species. Each of these is illustrated by several views of the shell.
The text is designed not only to enable biologists to identify species of testate amoebae, but to serve as an introduction to students interested in the taxonomy and biology of these freshwater protozoa. It will be of special interest to protozoologists, ecologists, limnologists, water treatment specialists and micropalaeontologists interested in recent sediments.

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Japanese earthworms: a synopsis of the
Megadrile species (Oligochaeta)

E. G. Easton

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British Museum (Natural History), London SW7 5BD

Contents

Introduction

Earthworms play an important part in the soil ecosystem where they participate in organic matter cycles and improve soil structure. They make nitrogen available for plant growth by feeding on organic material in the soil and voiding casts which have a low C/N ratio; in addition the casts contain fragmented litter which is readily broken down by micro-organisms to produce further nitrogen for plant growth. During ingestion the soil particles are ground down in size while the subsequent casts produce a turnover of the soil. Their burrows improve soil aeration and drainage. Although the activities of earthworms are beneficial to man, the worms may be vectors of protozoan, cestode or nematode parasites of mammals and birds which commonly infest pigs and poultry.

Earthworms may be very numerous in suitable habitats. One of the highest populations records was that of 845 individuals per square metre (total live weight 245 gm) from an orchard in Europe (Raw, 1959) and populations of 250 per square metre are frequently encountered in grasslands. Over 70 species of earthworms have been recorded from Japan and represent seven of the seventeen currently recognized families of the 'Megadrilacea'. In view of the importance of the group in soil fertility and their common occurrence, it is surprising that no comprehensive study has been published on the rich earthworm fauna of Japan. This situation has compelled the student needing to identify specimens, laboriously to search for matching descriptions scattered throughout the scientific literature beginning with Michaelsen's monograph (1900). A task made all the more difficult by numerous nomenclative changes which have taken place during the last 80 years. It is intended that the present work should go some way to make good this omission and provide a preliminary guide to the many species which have been reported. The Japanese species of the families Biwadrilidae, Lumbricidae, Ocnerodrilidae, Acanthodrilidae and Octochaetidae have been studied extensively but not so the species of the genus *Drawida* (family Moniligastridae) and of the *Pheretima* group of genera (*Amynthas, Metaphire, Pheretima, Pithemera* and *Poly-*

Bull. Br. Mus. nat. Hist. (Zool.) **40** (2) : 33–65   Issued 30 April 1980

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pheretima in the family Megascolecidae) which together constitute the majority of the Japanese earthworm fauna. The present synopsis brings together the records of all earthworms reported from Japan under their currently accepted names. Distributions within Japan and where appropriate, elsewhere in the world are also given. Diagnoses and keys are provided for the identification of all indigenous and introduced earthworms with the exception of the poorly known species of the genus *Drawida* for which only the diagnostic characters are tabulated. Information on species of the *Pheretima* group of genera is derived from current revisionary studies (Easton, 1979 and in preparation).

Geographical affinities of the earthworm fauna of Japan

The autochthonous (indigenous) species of the Japanese earthworm fauna have diverse origins and geographical affinities. Although Japan forms part of the Holoarctic geographical region, only one indigenous earthworm family, the Lumbricidae, has a holoarctic distribution. The Lumbricidae occur naturally in the eastern parts of North America and throughout the Palaearctic. The majority of species of this family have been recorded from the western Palaearctic; a few are known to be indigenous to Siberia and only a single species, *Eisenia japonica,* occurs naturally in Japan at the easternmost limit of the family range. The presence of indigenous taxa in both North America and the Palaearctic suggests that the family is of considerable antiquity, predating the formation of the North Atlantic during the Eocene. Several species of Lumbricidae are allochthonous (peregrine) and some, listed below (p. 35), have successfully colonized Japan, presumably after introduction by man.

Elements of the fauna of the Oriental Region are represented in Japan by eight species of the genus *Drawida,* family Moniligastridae, which is also present in Korea, Manchuria and eastern Siberia as well as most of the Oriental Region. The family Moniligastridae contains four other genera, these inhabit India and southeast Asia including the Philippines and the islands to the west of Wallace's line. It is apparently of recent Indian origin and has affinities with the African family Alluroididae (Jamieson, 1978). Possibly the family invaded Asia after the collision of the Indian and Asian plates during the Tertiary period.

The majority of the earthworms in Japan belong to the *Pheretima* group of genera (family Megascolecidae), the dominant earthworm group throughout southern mainland Asia, the Indo-Australasian Archipelago and the islands of the south-western Pacific. Most other Megascolecid genera occur in India or Australia and it has been suggested that the *Pheretima* group originated in the New Guinea/North Australia area and invaded Asia by way of the Indo-Australasian Archipelago during the Miocene or Oligocene (Easton, 1979). Several species of the *Pheretima* group are allochthonous, for example the Indonesian *Polypheretima elongata,* and have been introduced into Japan by man.

The family Biwadrilidae is of uncertain zoogeographical provenance being known from the single species *Biwadrilus bathybates* which is restricted to Japan and has the distinction of being the only member of the superfamily Biwadriloidea. This species has several primitive characters (male pores on segment 13; an unspecialized morphology and lateral lines) and is aquatic. Its Japanese distribution is considered to be a relict of a once, more widespread range (Sims, 1980).

Other Japanese species cannot be included in the groups discussed above. *Pontodrilus matsushimensis* (family Acanthodrilidae) is littoral and has also been recorded from New Caledonia and Chatham Island; it may occur on many other beaches of the Pacific. The four species included in the genus are found on beaches of the tropical and warmer temperate regions of the world. Three other genera recorded from Japan, *Ocnerodrilus* (Ocnerodrilidae), *Microscolex* (Acanthodrilidae) and *Dichogaster* (Octochaetidae) are allochthonous (not indigenous to the region) and have been introduced from tropical countries through the agency of man.

Classification and checklist of Japanese earthworms

(After Sims, in press)

Order Moniligastrida
      Family Moniligastridae
          Drawida hattamimizu Hatai, 1930
          D. japonica Michaelsen, 1892
          D. keikiensis Kobayashi, 1938
          D. koreana Kobayashi, 1938
          D. moriokaensis Ohfuchi, 1938
          D. nemora Kobayashi, 1936
          D. onfunatoensis Ohfuchi, 1938
          D. tairaensis Ohfuchi, 1938

Order Haplotaxida
  Suborder Lumbricina
    Superfamily Biwadriloidea
      Family Biwadrilidae
          Biwadrilus bathybates (Stephenson, 1917)
    Superfamily Lumbricoidea
      Family Lumbricidae
          Aporrectodea trapezoides species complex
              A. caliginosa (Savigny, 1826)
              A. trapezoides (Dùges, 1828)
          Bimastos parvus Eisen, 1874
          Dendrobaena octaedra (Savigny, 1826)
          Dendrodrilus rubidus (Savigny, 1826)
          Eisenia fetida (Savigny, 1826)
          E. japonica (Michaelsen, 1892)
          E. rosea (Savigny, 1826)
          Lumbricus sp.
    Superfamily Megascolecoidea
      Family Ocnerodrilidae
          Ocnerodrilus occidentalis Eisen, 1878
      Family Acanthodrilidae
          Microscolex phosphoreus (Dùges, 1837)
          Pontodrilus matsushimensis Iizuka, 1898
      Family Octochaetidae
          Dichogaster bolaui (Michaelsen, 1891)
          D. saliens (Beddard, 1893)
      Family Megascolecidae
          Amynthas acinctus (Goto & Hatai, 1899)
          A. corticus (Kinberg, 1867)
          A. flavescens (Goto & Hatai, 1898)
          A. glabrus (Gates, 1932)
          A. gracilis (Kinberg, 1867)
          A. habereri (Cognetti, 1906)
          A. hilgendorfi species-complex
              A. agrestis (Goto & Hatai, 1899)
              A. ambiguus (Cognetti, 1906)
              A. communissimus (Goto & Hatai, 1899)
              A. glandularis (Goto & Hatai, 1899)
              A. gomejimensis (Ohfuchi, 1937)
              A. hilgendorfi (Michaelsen, 1892)

A. irregularis (Goto & Hatai, 1899)
A. levis (Goto & Hatai, 1899)
A. rokugo (Beddard, 1892)
A. schizoporus (Goto & Hatai, 1898)
A. sieboldi lenzi (Michaelsen, 1899)
A. tappensis (Ohfuchi, 1935)
A. tokioensis (Beddard, 1892)
A. vittatus (Goto & Hatai, 1898)
A. yunoshimensis (Hatai, 1930)
A. hupiensis (Michaelsen, 1895)
A. illotus species-group
　　A. 'illotus' (Gates, 1932)
　　'Pheretima' oyuensis Ohfuchi, 1937
　　Amynthas pusillus (Ohfuchi, 1956)
A. japonicus (Horst, 1883)
A. megascolidioides (Goto & Hatai, 1899)
A. micronarius (Goto & Hatai, 1898)
A. minimus (Horst, 1893)
A. morrisi (Beddard, 1892)
A. obscurus (Goto & Hatai, 1898)
A. papulosus (Rosa, 1896)
A. parvicystis (Goto & Hatai, 1899)
A. robustus (Perrier, 1872)
A. scholasticus (Goto & Hatai, 1898)
Metaphire californica (Kinberg, 1867)
M. fuscata (Goto & Hatai, 1898)
M. hataii (Ohfuchi, 1937)
M. parvula (Ohfuchi, 1956)
M. peguana (Rosa, 1890)
M. riukiuensis (Ohfuchi, 1957)
M. schmardae (Horst, 1883)
M. servina (Hatai & Ohfuchi, 1937)
M. sieboldi (Horst, 1883)
M. tosaensis (Ohfuchi, 1938)
M. yamardai (Hatai, 1930)
M. yezoensis (Kobayashi, 1938)
Pheretima (Parapheretima) koellikeri Michaelsen, 1928
Pithemera bicincta (Perrier, 1875)
Polypheretima elongata (Perrier, 1872)
P. iizukai (Goto & Hatai, 1899)

Taxonomy

Key to the genera of earthworms recorded from Japan

1　Male pores in front of or at anterior margin of clitellum (Intestinal gizzards usually present)　　　2
　Male pores behind or at posterior margin of clitellum (Intestinal gizzards absent)　.　　.　　.　　3

2　Male pores on segment 10 or in furrow 10/11 (First of
　several intestinal gizzard in or before segment 13)　.　　.　　.　***DRAWIDA*** (family Moniligastridae)
　Male pores on segment 13* (Intestinal gizzards absent).　　.　　.　　.　　***BIWADRILUS*** (family
　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　　Biwadrilidae)

*The species *Eiseniella tetraedra* (Lumbricidae) may be confused with *Biwadrilus* since it has male pores on segment 13. Although it is a widespread peregrine species it has not yet been recorded from Japan. It may be distinguished from *Biwadrilus* by its more posteriorly placed clitellum (segments 22–37) and the possession of an intestinal gizzard and calciferous glands.

Male pores on segment 15 (A single intestinal gizzard in segments 17
or 17–18.   .   . *APORRECTODEA, BIMASTOS, DENDROBAENA, DENDRODRILUS,*
EISENIA and *LUMBRICUS* (family Lumbricidae)

3(1) Setae, 8 on each segment   4
Setae, more than 20 on each segment   .   .   .   . *PHERETIMA* group of genera (family
Megascolecidae)

4   Calciferous glands present   5
Calciferous glands absent   6

5   Calciferous glands in segment 9 or 9 and 10   .   *OCNERODRILUS* (family Ocnerodrilidae)
Calciferous glands in segments 15, 16 and 17   .   .   *DICHOGASTER* (family Octochaetidae)

6(4) Male pores on segment 17   .   .   .   .   .   .   *MICROSCOLEX* (family Acanthodrilidae)
Male pores on segment 18   .   .   .   .   .   .   *PONTODRILUS* family Acanthodrilidae)

Family MONILIGASTRIDAE

DRAWIDA Michaelsen, 1900

DIAGNOSIS. Setae lumbricine. Dorsal pores absent. Clitellum includes segments 10–13. Male pores in or near intersegmental furrow 10/11. Prostates absent. Oesophageal gizzards, calciferous glands and intestinal caeca absent. Several intestinal gizzards in segments 12–27. Excretory system holonephric.

INDIGENOUS DISTRIBUTION. Japan, Korea, Manchuria, Siberia, China, India, ?Ceylon, Burma, Thailand, Indo-China, Malaya, Philippines, Borneo.

REMARKS. Eight species of *Drawida* have been recorded from Japan. All are either restricted to Japan or also occur in Korea. [*D. japonica* has been recorded from outside the Japan/Korea area but Gates (1935: 3) is of the opinion that these records represent another species.]

Oishi (1932: 18) listed five new species of *Drawida* but omitted to characterize them. A survey of the literature failed to reveal any subsequent descriptions so they are *nomina nuda* which are therefore outside of nomenclature.

None of the eight species considered here is particularly well known and the specific status of each requires closer investigation. Since this appraisal would require consideration of their affinities with non-Japanese species, a project beyond the scope of the present work, only the principal morphological characters of these species are tabulated (Table 1).

Drawida hattamimizu Hatai, 1930

hattamimizu Hatai, 1930a : 485. Other Japanese records: Ohfuchi, 1938d : 1993; Kobayashi, 1941b : 263.

JAPANESE RECORDS. **Hokkaido,** ISHIKAI (Ohfuchi, 1938). **Honshu (Chūbu-Chihō)** (Kobayashi, 1941b), ISHIKAWA-KEN Hatta & Kanazawa (Hatai, 1930): **(Kinki-Chihō)** (Kobayashi, 1941b).

DISTRIBUTION. Japan.

Drawida japonica Michaelsen, 1892

japonica Michaelsen, 1892 : 232. Other Japanese records: Kobayashi, 1941b : 263,d: 458,e: 515.

JAPANESE RECORDS. 'Japan' (Michaelsen, 1892). **Honshu (Kantō-Chihō)** (Kobayashi, 1941b); TOCHII-KEN Utsunomiya (Kobayashi, 1941d): **(Chūbu-Chihō)** (Kobayashi, 1941b): **(Kinki-Chihō)** (Kobayashi, 1941b): **(Chūgoku-Chihō)** (Kobayashi, 1941b). **Shikoku** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b & e); NAGASAKI-KEN Iki (Kobayashi, 1941b).

DISTRIBUTION. Japan and Korea.

Table 1 *Drawida:* marker characters of Japanese species

Characters	moriokaensis	japonica	koreana	keikiensis	nemora	ofunatoensis	tairaensis	hattamimizu
Number of gizzards	2–3	2–3	2–3	3–4	3–5	4 or more	4	6–9
Segments with gizzards	10–13	12–13, 14	12–13, 14	12, 13–15	12, 13–15, 16	12–17, 18	13–19	13–19
Position of male pores	furrow 10/11	?	segment 10	furrow 10/11	furrow 10/11	furrow 10/11	furrow 10/11	furrow 10/11
Form of male pore	penis in copulatory pouch	porophore	porophore	penis in copulatory pouch	penis in copulatory pouch	penis in copulatory pouch	penis in copulatory pouch	?
Genital markings	–	vii–ix, occ. xii & xiii	vii–xii	–	vi–xiii	vi–xiii	viii	vi–xiii
Length (mm)	65–100	32–93	63–100	40–54	65–120	228–283	60–93	c. 246
Colour	dark lead grey; white ventrally	–	dark blue/ dark reddish blue	yellowish grey	dark blue; yellow grey ventrally	dark yellow; yellowish grey ventrally	fleshy red; white ventrally	?

In addition to the characters given above, the species *hattamimizu* is distinctive in having a clitellum extending from segment 9–15, occasionally 16 (other species segments 10–13) and spermathecal pores slightly ventral to *d* (other species *c* or median to *c*).

Drawida keikiensis Kobayashi, 1938

keikiensis Kobayashi, 1938*a* : 107. Japanese records: Kobayashi, 1941*b* : 263.

JAPANESE RECORDS. **Honshu (Chūbu-Chihō)** (Kobayashi, 1941*b*): **(Kinki-Chihō)** (Kobayashi, 1941*b*): **(Chūgoku-Chihō)** (Kobayashi, 1941*b*). **Shikoku** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b*).

DISTRIBUTION. Japan and Korea.

Drawida koreana Kobayashi, 1938

koreana Kobayashi, 1938*a* : 102. Japanese records: Kobayashi, 1941*e* : 515.

JAPANESE RECORDS. **Kyushu** (Kobayashi, 1941*e*).

DISTRIBUTION. Japan and Korea.

Drawida moriokaensis Ohfuchi, 1938

moriokaensis Ohfuchi, 1938*b* : 44.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** IWATE-KEN Morioka (Ohfuchi, 1938); MIYAGI-KEN Tsukinoki (Ohfuchi, 1938).

DISTRIBUTION. Japan.

Drawida nemora Kobayashi, 1936

nemora Kobayashi, 1936 : 141. Japanese records: Kobayashi, 1941*b* : 263.

JAPANESE RECORDS. **Honshu (Chūbu-Chihō)** (Kobayashi, 1941*b*).

DISTRIBUTION. Japan and Korea.

Drawida ofunatoensis Ohfuchi, 1938

ofunatoensis Ohfuchi, 1938*b* : 33.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** IWATE-KEN coast & islands of Sanriku (Ohfuchi, 1938*b*); MIYAGI-KEN some regions of coast (Ohfuchi, 1938*b*).

DISTRIBUTION. Japan.

Drawida tairaensis Ohfuchi, 1938

tairaensis Ohfuchi, 1938*b* : 39.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** AKITA-KEN Honjō (Ohfuchi, 1938*b*); IWATE-KEN Morioka (Ohfuchi, 1938*b*); MIYAGI-KEN Tsukinoki (Ohfuchi, 1938*b*); FUKUSHIMA-KEN Taira machi (Ohfuchi, 1938*b*).

DISTRIBUTION. Japan.

Family BIWADRILIDAE

BIWADRILUS Jamieson, 1971

DIAGNOSIS. Setae lumbricine. Dorsal pores absent. Clitellum includes segments 15–31. Prostates absent. Male pores on segment 13. Oesophageal gizzards, intestinal gizzards, calciferous glands and intestinal caeca absent. Excretory system holonephric.

INDIGENOUS RANGE· Japan.

Biwadrilus bathybates (Stephenson, 1917)

Criodrilus bathybates Stephenson, 1917 : 96. Other Japanese records: (syn. *miyashitai*) Yamaguchi, 1953 : 309.

C. miyashitai Nagase & Nomura, 1937 : 361.

DIAGNOSIS. As for the genus.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** YAMAGATA-KEN Tsuruoka (Nagase & Nomura, 1937): **(Chūbu-Chihō)** KYOTO-KEN Biwa-ko (Stephenson, 1917; Yamaguchi, 1953); KYOTO-FU Komori (Nagase & Nomura, 1937); OSAKA-FU Minamitoyoshima (Yamaguchi, 1953): **(Kinki-Chihō)** HYOGO-KEN Muko (Yamaguchi, 1953).

DISTRIBUTION. Japan.

Family LUMBRICIDAE

DIAGNOSIS. Setae lumbricine. Dorsal pores present. Clitellum usually begins behind segment 22, rarely (*Eiseniella*) segment 15. Male pores usually on segment 15, rarely (*Eiseniella*) segments 12, 13 or 14. Prostates, oesophageal gizzards and intestinal caeca absent. A single intestinal gizzard in segment 17 or 17 and 18. Excretory system holonephric.

INDIGENOUS RANGE. Palaearctic and eastern North America.

REMARKS. The currently recognized Lumbricid genera are defined principally on difficult to observe somatic structures. Since the Japanese species can be readily identified without recourse to these characters, generic diagnoses are not provided.

Of the eight Lumbricid species recorded from Japan, seven are widespread allochthonous forms which may have been introduced into Japan through the agency of man. Only one species, *Eisenia japonica* is thought to be indigenous but even this species has been recorded in Europe (Graff, 1954). Full descriptions and distributions of the allochthonous species were provided by Gates (1972a). For a detailed description of *E. japonica* see Gates (1975).

The names *Bimastos, E. fetida* were emended to *Bimastus* and *E. foetida* respectively by Michaelsen (1900) and used by many subsequent authors. Under the articles of the International Code of Zoological Nomenclature such emendations are invalid and the original orthography is employed here.

Several recent revisions of the family Lumbricidae (Omodeo, 1956; Bouché, 1972, Perel, 1976) include taxonomic changes which effect the Japanese fauna. The genus *Allolobophora* has been restricted to include only the type species (*A. chlorotica*); excluded species being accommodated in either *Eisenia* or *Aporrectodea* (syn. *Nicodrilus* Bouché). The species *Bimastos tenuis* has been placed within the synonymy of *rubida* which itself has been transferred from *Dendrobaena* to *Dendrodrilus*.

Some of the results of these revisions are incompatible with one another and with the results of other workers. Often a species is consigned to different genera by different workers. Of the Japanese species, *rosea* is included in *Eisenia* for convenience although Perel (1974) excluded it from this genus but did not indicate to which genus it should be assigned.

Key to the species of Lumbricidae of Japan

1 Prostomium tanylobic   .   .   .   .   *Lumbricus*
   Prostomium epilobic   2

2 Setae closely paired ($aa = 3ab$)   3
   Setae widely paired ($aa = 1-2ab$)   4

3 Tubercula pubertatis on segments 24, 25, 26–30 or absent .   .   .   .   .   *Bimastos parvus*
   Tubercula pubertatis on segments 27–29   .   .   .   .   *Eisenia japonica*
   Tubercula pubertatis on segments 28–30, 31 .   .   .   .   *Eisenia fetida*
   Tubercula pubertatis on segments 29, 30–31 .   .   .   .   *Eisenia rosea*
   Tubercula pubertatis on segments 31–33   .   .   *Aporrectodea trapezoides* species-complex

4(2) Tubercula pubertatis on segments 28, 29–30, 31 (tail cylindrical) . ***Dendrodrilus rubidus***
Tubercula pubertatis on segments 31–33 (tail octogonal) . . . ***Dendrobaena octaedra***

Aporrectodea trapezoides species-complex

trapezoides species-group, Gates, 1972*b* : 1.

DIAGNOSIS. Length 60–140 mm. Body cylindrical or flattened posteriorly to form rectangular cross section with setal pairs at corners. Prostomium epilobic. Clitellum on segments 27, 28, 29–33, 34, 35. Tubercula pubertatis on segments 31–33. Male pores on segment 15. Spermathecal pores in furrows 9/10/11 in setal line *c*. First dorsal pore in a furrow between 6/7 and 13/14. Setae closely paired, setal ratio (*caliginosa*) $30aa = 10ab = 20bc = 7cd = 100dd$.

REMARKS. The close affinities of the component taxa of this complex were first recognized by Gates (1972*b*) when he erected the species-complex to accommodate *caliginosa* Savigny, 1826 (under the name *turgida* Eisen, 1873), *trapezoides* Dùges, 1828 and six other species.

Aporrectodea caliginosa (Savigny, 1826)

caliginosa Savigny, 1826 : 180. Japanese records: Kobayashi, 1941*a* : 52, *b* : 264, *c* : 378, *e* : 515; Nakamura, 1967 : 164; Nakamura, 1972 : 18; Nakamura, 1973*a* : 199, *b* : 210.

DIAGNOSIS. Length 60–85 mm. Body cylindrical, unpigmented, anterior segments flesh pink, rest of body pale grey. Clitellum on segments 27, 28, 29–34, 35. Genital tumescences incorporating setae *a* and *b* on segments 9–11, 30, 32–34 and frequently 27. First dorsal pore in furrow 12/13 or 13/14.

JAPANESE RECORDS. **Hokkaido** (Nakamura, 1972); ISHIKAI Sapporo (Nakamura, 1967; 1973*a* & *b*). **Honshu** (**Ōu-Chihō**) (Kobayashi, 1941*c*): (**Chūbu-Chihō**) (Kobayashi, 1941*b* & *c*): (**Kinki-Chihō**) (Kobayashi, 1941*b* & *c*): (**Chūgoku-Chihō**) (Kobayashi, 1941*b* & *c*); SHIMANE-KEN Oki-guntō (Kobayashi, 1941*a*). **Shikoku** (Kobayashi, 1941*b* & *c*). **Kyushu** (Kobayashi, 1941*b*, *c* & *e*); KAGOSHIMA-KEN Shibushi & Yanakawa (Kobayashi, 1941*c*).

DISTRIBUTION. Cosmopolitan (indigenous to Palaearctic).

Aporrectodea trapezoides (Dùges, 1828)

trapezoides Dùges, 1828 : 289. Japanese records: Michaelsen, 1892 : 230; Kobayashi, 1938*b* : 414; Kobayashi, 1941*b* : 264, *d* : 459, *e* : 515.

DIAGNOSIS. Length 80–140 mm. Body flattened posteriorly to form rectangular cross section with setal pairs at corners, slate, brown, reddish brown, often paler ventrally. Clitellum on segments 27, 28–33, 34. Genital tumescences incorporating setae *a* and *b* on segments 9–11, 32–34 often 27 and occasionally 26, 28, 29. First dorsal pore in a furrow between 6/7 and 13/14.

JAPANESE RECORDS. 'Japan' (Michaelsen, 1892). **Hokkaido** (Kobayashi, 1941*b* & *c*); OSHIMA Hakodate (Kobayashi, 1938*c*). **Honshu** (**Kantō-Chihō**) TOCHII-KEN Utsunomiya (Kobayashi, 1941*d*): (**Kinki-Chihō**) (Kobayashi, 1941*b*): (**Chūgoku-Chihō**) (Kobayashi, 1941*b*). **Shikoku** (Kobayashi, 1941*b*). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b* & *e*).

DISTRIBUTION. Palaearctic (indigenous), Nearctic, Oriental, Australasian and Neotropical regions.

Bimastos parvus Eisen, 1874

parvus Eisen, 1874 : 46. Japanese records: Michaelsen, 1910 : 64; Kobayashi, 1941*a* : 52, *b* : 264, *c* : 378, *e* : 515; Yamaguchi, 1953 : 310; Gates, 1972*a* : 87.
beddardi Michaelsen, 1894 : 182. Japanese records: Kobayashi, 1941*b* : 264, *e* : 515.

DIAGNOSIS. Length 17–65 mm. Body cylindrical, reddish dorsally, yellow ventrally. Prostomium epilobic. Clitellum on segments 23, 24, 25–31, 32. Tubercula pubertatis absent or in the form of indistinct paired longitudinal ridges along the ventral margins of the clitellum on segments 24, 25, 26–30. Male pores on segment 15. Spermathecal pores absent. First dorsal pore in furrow 5/6. Setae closely paired, setal ratio (postclitellar segments) $30aa = 10ab = 25bc = 9cd = 100dd$.

JAPANESE RECORDS. 'Japan' (Michaelsen, 1910—intercepted at Hamburg; Gates, 1972—intercepted at American port). **Hokkaido** (Kobayashi, 1941c); ISHIKAI Chitose (Yamaguchi, 1953). **Honshu (Ōu-Chihō)** (Kobayashi, 1941b): **(Chūbu-Chihō)** (Kobayashi, 1941b & c): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c); SHIMANE-KEN Oki-guntō (Kobayashi, 1941a & b). **Shikoku** (Kobayashi, 1941b & c). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b, c & e); NAGASAKI-KEN Gottō-rettō & Iki (Kobayashi, 1941b); KAGOSHIMA-KEN Kagoshima & Shibushi (Kobayashi, 1941c).

DISTRIBUTION. Cosmopolitan (indigenous to eastern North America).

Dendrobaena octaedra (Savigny, 1826)

octaedra Savigny, 1826 : 183; Gates, 1974a : 15. Japanese records: Nakamura, 1967 : 164; Stöp-Bowitz, 1969 : 214; Tamura et al, 1969 : 26; Nakamura, 1972 : 18; Nakamura, 1973a : 199, b : 210.

DIAGNOSIS. Length 17–40 mm. Body cylindrical, octagonal posteriorly, red, yellowish, brown, violet or copper coloured. Prostomium epilobic. Clitellum on segments 27, 28, 29–33, 34. Tubercula pubertatis in form of a longitudinal ridge on segments 31–33. Male pores on segment 15. Spermathecal pores in furrows 9/10/11/12 at seta d. First dorsal pore in a furrow between 4/5 and 6/7. Setae widely paired, $aa = ab = bc = cd$, dd slightly greater than aa.

JAPANESE RECORDS. **Hokkaido** Stöp-Bowitz, 1969; Nakamura 1972); ISHIKAI Sapporo (Nakamura, 1967; 1973a & b); HIDAKA Hidaka-Mombetsu (Tamura et al, 1969).

DISTRIBUTION. Palaearctic (indigenous), Nearctic and Oriental regions.

Dendrodrilus rubidus (Savigny, 1826)

rubida Savigny, 1826 : 182.
tenuis Eisen, 1874 : 44. Japanese records: Kobayashi, 1938b : 415; Kobayashi, 1941b : 264; Stöp-Bowitz, 1969 : 227; Tamura et al, 1969 : 26; Nakamura, 1972 : 18; Nakamura, 1973a : 199, b : 210.

DIAGNOSIS. Length 20–90 mm. Body cylindrical, dark red dorsally, pale ventrally and dorsally in the intersegmental furrows. Prostomium epilobic. Clitellum on segments 24, 25, 26, 27–31, 32. Tubercula pubertatis absent or in the form of indistinct paired longitudinal ridges on segments 28, 29–30, 31. Male pores on segment 15. Spermathecal pores absent or in furrows 9/10/11 in setal line c. First dorsal pore in furrow 4/5 or 5/6. Setae widely paired, $18aa = 10ab = 24bc = 12cd = 50dd$.

JAPANESE RECORDS. **Hokkaido** (Kobayashi, 1941b; Stöp-Bowitz, 1969; Nakamura, 1972); ISHIKAI Sapporo (Nakamura, 1973a & b); HIDAKA Hidaka-Mombetsu (Tamura et al, 1969); OSHIMA Hakodate & Nanayehama (Kobayashi, 1938c). **Honshu (Chūbu-Chihō)** (Kobayashi, 1941b): **(Chūgoku-Chihō)** (Kobayashi, 1941b).

DISTRIBUTION. Cosmopolitan (indigenous to Palaearctic).

Eisenia fetida (Savigny, 1826)

fetida Savigny, 1826 : 182. Japanese records: Michaelsen, 1892 : 230; Sasaki, 1924 : 89; Kobayashi, 1928 : 468; Kobayashi, 1938b : 415; Ohfuchi, 1938d : 1992; Kobayashi, 1941b : 263, c : 378, d : 459, e : 515; Stöp-Bowitz, 1969 : 210; Nakamura, 1972 : 18; Nakamura, 1973a : 199, b : 210.

DIAGNOSIS. Length 35–130 mm. Body cylindrical, reddish purple or brown dorsally, yellow in intersegmental furrows and ventrally. Prostomium epilobic. Clitellum on segments 24, 25, 26–32. Tubercula pubertatis in the form of paired longitudinal ridges on segments 28–30, 31. Male pores on segment 15. Spermathecal pores in furrows 9/10/11, near the dorsal line. First dorsal pores in furrow 5/6. Setae closely paired, $4aa = ab = 4bc = cd = 16dd$.

JAPANESE RECORDS. 'Japan' (Michaelsen, 1892). **Hokkaido** (Kobayashi, 1941b & c; Stöp-Bowitz, 1969; Nakamura, 1972); ISHIKAI (Ohfuchi, 1938) Sapporo (Nakamura, 1973a & b); OSHIMA Hakodate (Kobayashi, 1938c). **Honshu** (Ōu-Chihō) (Kobayashi, 1941b & c); AOMORI-KEN Aomori (Sasaki, 1924); IWATE-KEN Morioka (Sasaki, 1924); MIYAGI-KEN Sendai (Sasaki, 1924; Kobayashi, 1928): **(Kantō-Chihō)** (Kobayashi, 1941b); TOCHII-KEN Utsunomiya (Kobayashi, 1941d); TOKYŌ-TO Tokyo (Sasaki, 1924): **(Chūbu-Chihō)** (Kobayashi, 1941b & c): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c). **Shikoku** (Kobayashi, 1941b & c). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b, c & e); NAGASAKI-KEN Iki (Kobayashi, 1941b); KAGOSHIMA-KEN Kagoshima, Shibushi & Yanakawa (Kobayashi, 1941c). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941b & c).

DISTRIBUTION. Cosmopolitan (indigenous to Palaearctic)

Eisenia japonica (Michaelsen, 1892)

japonica Michaelsen, 1892 : 230. Other Japanese records: Michaelsen, 1900 : 481; Michaelsen, 1910 : 62; Kobayashi, 1938b : 414; Oishi, 1934 : 134; Kobayashi, 1941a : 52, b : 264, c : 378, d : 460, e : 515; Nakamura, 1967 : 164; Tamura et al, 1969 : 26; Nakamura, 1971 : 347; Nakamura, 1972 : 10; Nakamura, 1973a : 199, b : 210; Gates, 1975 : 1.
japonica f. *gigantica* Oishi, 1934 : 134. Other Japanese records: Kobayashi, 1941b : 264.
japonica f. *minuta* Oishi, 1934 : 134.

DIAGNOSIS. Length 24–175 mm. Body cylindrical, whitish grey or dark reddish brown. Prostomium epilobic. Clitellum on segments 23, 24–31. Tubercula pubertatis in the form of paired longitudinal ridges on segments 27–29, often disrupted and on segments 27 and 29 only. Male pores on segment 15. Spermathecal pores in furrows 9/10/11 in setal line *c*. First dorsal pore in furrow 4/5. Setae closely paired, setal ratio $93aa = 10ab = 46bc = 7cd = 310dd$.

REMARKS. Some authors (Beddard, 1895; Oishi, 1934; Kobayashi, 1941; Nakamura, 1972) have recognized varieties of this species. Their taxonomic validities are dubious nevertheless the diagnostic features tabulated by Kobayashi (1941f) are given below (Table 2).

JAPANESE RECORDS. **Hokkaido** (Kobayashi, 1941b & c; Nakamura, 1972); ABASHIRI Oketo (Nakamura, 1971); KAMIKAWA Furano & Mitsumata (Gates, 1975), Monomanai & Nishi-Shibetsu (Nakamura, 1971); ISHIKAI Misumai, near Sapporo (Nakamura, 1973a), Sapporo (Nakamura, 1967, 1973a & b); HIDAKA Hidaka-Mombetsu (Tamura et al, 1969); SHIRIBESHI Kutchan & Yotei-zan (Gates, 1975); OSHIMA Hakodate (Michaelsen, 1892); Nanayehama & Hakodate (Kobayashi, 1938c). **Honshu** (Ōu-Chihō) (Kobayashi, 1941b & c): **(Kantō-Chihō)** (Kobayashi, 1941b); TOCHII-KEN Utsunomiya (Kobayashi, 1941d); KANAGAWA-KEN Eno-shima (Michaelsen, 1892*; Rosa, 1893); Yokohama (Michaelsen, 1910): **(Chūbu-Chihō)** (Kobayashi, 1941b & c); YAMANASHI-KEN Fuji-san (Michaelsen, 1900): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c); SHIMANE-KEN Oki-guntō (Kobayashi, 1941a & b). **Shikoku** (Kobayashi, 1941b & c). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b, c & e); FUKUOKA-KEN Moji (Michaelsen, 1910); NAGASAKI-KEN Iki (Kobayashi, 1941b); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941c); KAGOSHIMA-KEN Kagoshima (Kobayashi, 1941c).

DISTRIBUTION. Palaearctic (Japan, Korea and Europe).

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*Michaelsen's original reference to this record was 'Enoshima, Japan'. It is uncertain which of the localities named Enoshima was referred to but Rosa (1893) noted that it was near Tokyo.

Table 2 *Eisenia japonica*: marker characters of varieties. (After Kobayashi, 1941*f*)

	minuta	*typica*	*gigantica*
Length (mm)	24–55	42–102	139–175
Diameter (mm)	1·75–2·80	2·5–5·0	3·5–7·2
Segment number	85–110	96–140	125–151
Colour	uniformly whitish grey	anterior pink, posterior whitish grey	dark reddish brown
Shape of tubercula pubertatis	round	triangular	intermediate
Size of seta (μ)	290 × 24	390 × 36	540 × 47

Eisenia rosea Savigny, 1826)

rosea Savigny, 1826 : 182; Gates, 1974*b* : 9. Japanese records: Nakamura, 1971 : 347; Nakamura, 1972 : 18; Nakamura, 1973*a* : 199, *b* : 210.

DIAGNOSIS. Length 25–85 mm. Body cylindrical, unpigmented, anterior segments dark red, rest of body pink or pinkish grey. Prostomium epilobic. Clitellum on segments 24, 25, 26–32, 33. Tubercula pubertatis on segments 29–30, 31. Male pores on segment 15. Spermathecal pores in furrows 9/10/11, near dorsal line or halfway between lateral line and setal line *d*. First dorsal pore in furrow 4/5. Setae closely paired, *aa* greater than *bc*, *ab* greater than *cd, dd* = 1/3–1/2 body circumference.

JAPANESE RECORDS. **Hokkaido** (Nakamura, 1972); KAMIKAWA Monomanai & Nishi-Shibetsu (Nakamura, 1971); ISHIKAI Hiroshima (Nakamura, 1973*a*); Sapporo (Nakamura, 1973*b*).

DISTRIBUTION. Cosmopolitan (indigenous to Palaearctic)

LUMBRICUS Linnaeus, 1758

Lumbricus sp. Ohfuchi, 1941 : 255.

DIAGNOSIS. Length 20–300 mm. Body cylindrical, trapezoidal posteriorly, purplish red or purplish brown dorsally, paler ventrally. Prostomium prolobic. Clitellum begins between segment 26 and 39 and occupies 5–15 segments. Tubercula pubertatis usually occupies more than 4 clitellar segments. Male pores on segment 15. Spermathecal pores in furrows 9/10/11 between setae *c* and *d*. First dorsal pore between furrows 5/6 and 9/10. Setae closely paired.

JAPANESE RECORDS. **Honshu (Chūgoku-Chihō)** YAMAGUCHI-KEN Shuhodo Akigoshi (Ohfuchi, 1941).

DISTRIBUTION. Cosmopolitan (indigenous to Holarctic).

Family OCNERODRILIDAE

OCNERODRILUS Eisen, 1878

DIAGNOSIS. Setae lumbricine. Dorsal pores absent. Clitellum includes segments 14–19. Prostates tubular, discharging through combined male and prostatic pores on segment 17. Oesophageal and intestinal gizzards absent. Calciferous glands in segment 9 or segments 9 and 10. Intestinal caeca absent. Excreatory system holonephric.

INDIGENOUS RANGE. Tropical and subtropical America, tropical Africa. Several species are allochthonous, one, *O. occidentalis* Eisen, 1878 has been recorded from Japan.

Ocnerodrilus occidentalis Eisen, 1878

occidentalis Eisen, 1878 : 10. Japanese records: Kobayashi, 1941*a* : 52, *b* : 263, *c* : 378, *e* : 515; Gates, 1973 : 16.

DIAGNOSIS. As for the genus.

JAPANESE RECORDS. 'Japan' (Gates, 1973 interception at American port).   **Honshu (Kantō-Chihō)** KANAGAWA-KEN Ō-shima (Kobayashi, 1941*b* & *c*): **(Chūbu-Chihō)** (Kobayashi, 1941*b* & *c*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*): **(Chūgoku-Chihō)** (Kobayashi, 1941*b* & *c*); SHIMANE-KEN Oki-guntō (Kobayashi, 1941*a* & *b*).   **Shikoku** (Kobayashi, 1941*b* & *c*). **Kyushu** (Kobayashi, 1941*b*, *c* & *e*); NAGASAKI-KEN Gottō-rettō (Kobayashi, 1941*b*); KAGOSHIMA-KEN Kagoshima & Yanakawa (Kobayashi, 1941*c*).   **Okinawa-guntō** OKINAWA-JIMA (Kobayashi, 1941*b* & *c*).

DISTRIBUTION. Palaearctic, Nearctic, Oriental and Ethiopian regions.

Family ACANTHODRILIDAE

MICROSCOLEX Rosa, 1887

DIAGNOSIS˙ Setae lumbricine. Dorsal pores absent. Clitellum includes segments 14–16. Prostates tubular, discharging near male pores on segment 17. A weak oesophageal gizzard in segment 5. Calciferous glands, intestinal caeca and intestinal gizzards absent. Excretory system holonephric.

INDIGENOUS RANGE. Southern South America, South Africa, Sub-Antarctic Islands. Two species, *M. dubius* (Fletcher, 1887) and *M. phosphoreus* (Dugès, 1837) are allochthonous, the latter has been recorded from Japan.

Microscolex phosphoreus (Dugès, 1837)

phosphoreus Dugès, 1837 : 17. Japanese records: Yamaguchi, 1935 : 200; Kobayashi, 1941*b* : 263.

DIAGNOSIS. As for the genus.

JAPANESE RECORDS.   **Honshu (Kantō-Chihō)** (Kobayashi, 1941*b*): **(Chūgoku-Chihō)** (Kobayashi 1941*b*).   **Shikoku** (Kobayashi, 1941*b*).   **Kyushu** KAGOSHIMA-KEN Ōsio (Yamaguchi, 1935).

DISTRIBUTION. Cosmopolitan (? indigenous in South America).

PONTODRILUS Perrier, 1874

DIAGNOSIS. Setae lumbricine. Dorsal pores absent. Clitellum begins on segment 14 and occupies 5 or 6 segments. Prostates tubular discharging through combined male and prostatic pores on segment 18. Oesophageal gizzard rudimentary or absent. Calciferous glands, intestinal caeca and intestinal gizzards absent. Excretory system holonephric.

DISTRIBUTION. Circum-mundane, on sea shores throughout the tropics and warmer areas of the temperate zones. A single species has been recorded from Japan.

Pontodrilus matsushimensis Iizuka, 1898

matsushimensis Iizuka, 1898 : 21. Other Japanese records: Yamaguchi, 1953 : 309.

DIAGNOSIS. As for the genus.

JAPANESE RECORDS.   **Honshu (Ōu-chihō)** MIYAGI-KEN Matsushima-wan (Iizuka, 1898); Miyakojima (Yamaguchi, 1953): **(Kinki-Chihō)** HYOGO-KEN Akashi (Yamaguchi, 1953).   **Kyushu** FUKUOKA-KEN Fukuoshima (Yamaguchi, 1953); 'shore of Ranshima near Ogura' (Yamaguchi, 1953).

DISTRIBUTION. Japan, New Caledonia (Beddard, 1899) and Chatham Island, New Zealand (as var. *chathamianus* Michaelsen, 1899).

Family OCTOCHAETIDAE
DICHOGASTER Beddard, 1888

DIAGNOSIS. Setae lumbricine. Dorsal pores present. Clitellum includes segments 14–18. Prostates tubular discharging on segments 17 and 19 or 17 only. Male pores on segment 18. Penial setae present. Two well developed oesophageal gizzards anterior to septum 8/9. Paired calciferous glands in segments 15, 16 and 17, intestinal caeca and gizzards absent. Excretory system meronephric.

INDIGENOUS RANGE. Tropical Americas, Africa. Several species are allochthonous of which two have been recorded from Japan.

Key to species recorded from Japan

1   One pair of prostates which discharge onto segment 17   .   .   .   .   *saliens*
    Two pairs of prostates which discharge onto segments 17 and 19   .   .   .   .   .   *bolaui*

Dichogaster bolaui Michaelsen, 1891

bolaui Michaelsen, 1891a : 9. Japanese records: Kobayashi, 1941c : 379.

DIAGNOSIS. Length 20–40 mm. Two pairs of prostates discharging on segments 17 and 19.

JAPANESE RECORDS.   **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941c).

DISTRIBUTION. Cosmopolitan (indigenous range unknown).

Dichogaster saliens (Beddard, 1893)

saliens Beddard, 1893 : 683.
hatomaana Ohfuchi, 1957 : 259.

DIAGNOSIS. Length 17–70 mm. One pair of prostates discharging onto segment 17 only.

REMARKS. The description of *D. hatomaana* provided by Ohfuchi (1957) is indistinguishable from that of *saliens.*

JAPANESE RECORDS.   **Sakishima-Guntō** IRIOMOTE-JIMA Hatoma-jima (Ohfuchi, 1957).

DISTRIBUTION. Cosmopolitan (indigenous range unknown).

Family MEGASCOLECIDAE
PHERETIMA group of genera

DIAGNOSIS. Setae perichaetine. Dorsal pores present. Clitellum including segments 14–16. Prostates racemose discharging through combined male and prostatic pores on segment 18 or rarely 19. Oesophageal gizzard single, well developed in segment 8. Calciferous glands absent. Intestinal caeca usually present. Excretory system meronephric.

INDIGENOUS RANGE. Japan, Korea, China, Burma (east of the Chinwin/Irrawaddy axis), Thailand, Vietnam, Malaysia, Indonesia, Philippines, Papua New Guinea, New Britain, New Hebrides, New Caledonia, northern Queensland, islands of the western Pacific (Easton, 1979).

REMARKS. Nine closely related genera comprising about 760 nominal species, are included in the *Pheretima* group of genera. Five have been recorded from Japan: *Amynthas* Kinberg, 1867; *Metaphire* Sims & Easton, 1972; *Pithemera* Sims & Easton, 1972; *Pheretima* Kinberg, 1867; and *Polypheretima* Michaelsen, 1934.

GENERIC DIAGNOSES

Polypheretima—Intestinal caeca absent.

Pithemera—One pair of intestinal caeca present originating in or near segment 22.

Amynthas—One pair of intestinal caeca present originating in or near segment 27; male pores superficial.

Metaphire—One pair of intestinal caeca present originating in or near segment 27; male pores in copulatory pouches; no nephridia present on spermathecal ducts.

Pheretima—One pair of intestinal caeca present originating in or near segment 27; male pores in copulatory pouches; nephridia present on spermathecal ducts.

For full generic descriptions and keys to nominal species and species-groups see Sims & Easton, 1972 (also Easton, 1979 for keys and descriptions of the species of *Polypheretima*).

Key to the species of Megascolecidae of Japan

1	Intestinal caeca absent	2
	Intestinal caeca present	3
2	Spermathecal pores absent or in furrows 5/6/7, 5/6 or 6/7; genital markings presetal	*Polypheretima elongata*
	Spermathecal pores in furrows 5/6/7/8/9; genital markings postsetal	*Polypheretima iizukaii*
3(1)	Intestinal caeca originate in segment 22	*Pithemera bicincta*
	Intestinal caeca originate in segments 25–27	4
4	Spermathecal pores absent	5
	Spermathecal pores present	6
5	Intestinal caeca simple	*Amynthas illotus* species-group
	Intestinal caeca manicate	*Amynthas hilgendorfi* species-complex (part)
6(4)	Spermathecal pores segmental	7
	Spermathecal pores intersegmental	9
7	Spermathecal pores presetal	*Amynthas parvicystis*
	Spermathecal pores postsetal	8
8	Spermathecal pores on segment 6	*Amynthas glabrus*
	Spermathecal pores on segments 6, 7 & 8	*Amynthas obscurus*
9(6)	First spermathecal pores in furrow 4/5	10
	First spermathecal pores in furrow 5/6	11
	First spermathecal pores in furrow 6/7	22
	First spermathecal pores in furrow 7/8	29
10	Four pairs of spermathecal pores; male pores on segment 18	*Amynthas scholasticus*
	Five pairs of spermathecal pores; male pores on segment 19	*Amynthas megascolidioides*
11(9)	One pair of spermathecal pores	*Amynthas minimus*
	Two pairs of spermathecal pores	*Amynthas morrisi*
	Three pairs of spermathecal pores	12
	Four pairs of spermathecal pores	17
12	Intestinal caeca simple	13
	Intestinal caeca manicate	16
13	Male pores superficial	14
	Male pores in copulatory pouches	*Metaphire yezoensis*
14	Male porophores small; genital markings present	15
	Male porophores large: genital markings absent	*Amynthas acinctus*

15 Genital markings in transverse rows (body length
    less than 80 mm) . . . . *Amynthas papulosus*
    Genital markings in clusters associated with male pores
    (body length up to 200 mm) . . . . *Amynthas gracilis*

16(12) Male pores superficial or absent . . . *Amynthas hilgendorfi* species-complex (part)
        Male pores in copulatory pouches . . . . *Metaphire hataii*

17(11) Intestinal caeca simple 18
        Intestinal caeca manicate . . . . *Amynthas habereri*

18 Male pores superficial 19
    Male pores in copulatory pouches 20
    Male pores in seminal grooves . . . . *Metaphire riukiuensis*[1] (part)

19 Genital markings small, segmental . . . . *Amynthas corticus*
    Genital markings large, intersegmental . . . . . *Amynthus micronarius*

20(18) Genital markings present . . . . *Metaphire fuscata*
        Genital markings absent 21

21 Copulatory pouches restricted to segment 18 . . . . . *Metaphire tosaensis*
    Copulatory pouches extending onto segments 17 and 19 . *Metaphire riukiuensis*[1] (part)

22(9) One thecal segment . . . . . *Amynthas hilgendorfi* species-complex (part)
       Two thecal segments 23
       Three thecal segments 25

23 Male pores in seminal grooves . . . . *Amynthas japonicus*
    Male pores simple or absent . . . *Amynthas hilgendorfi* species-complex (part)
    Male pores in copulatory pouches 24

24 Intestinal caeca simple . . . . *Metaphire parvula*
    Intestinal caeca manicate . . . . *Pheretima koellikeri*

25(22) Intestinal caeca simple 26
        Intestinal caeca manicate 28

26 Male pores superficial 27
    Male pores in copulatory pouches . . . . *Metaphire peguana*

27 Genital markings segmental . . . . *Amynthas flavescens*
    Genital markings intersegmental at 17/18 and 18/19 . . . *Amynthas hupiensis*

28(25) Genital markings paired, median to male pores . . . . *Metaphire servina*
        Genital markings numerous, within copulatory pouches . . *Metaphire yamardai*
        Genital markings absent . . . . *Metaphire sieboldi*

29(9) One thecal segment . . . . . *Amynthas hilgendorfi* species-complex (part)
       Two thecal segments 30

30 Male pores superficial; genital markings present . . . . *Amynthas robustus*
    Male pores in copulatory pouches; genital markings absent 31

31 Intestinal caeca simple . . . . *Metaphire californica*
    Intestinal caeca manicate . . . . *Metaphire schmardae*

Amynthas acinctus (Goto & Hatai, 1899)

acincta Goto & Hatai, 1899 : 16. Other Japanese records: Yamaguchi, 1930*a* : 52; Ohfuchi,
    1938*d* : 1933; Kobayashi, 1941*b* : 260; Yamaguchi, 1962*a* : 10.
?phaselus Hatai, 1930*b* : 659. Other Japanese records: Kobayashi, 1938*b* : 410; Kobayashi,
    1941*b* : 260, *e* : 513; Yamaguchi, 1962*a* : 11.
?maculosus Hatai, 1930*b* : 661.

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[1]It is uncertain whether the male pores of *M. riukiuensis* are in copulatory pouches or in seminal grooves. The species has been keyed out twice to allow for either condition.

?kamitai Kobayashi, 1934 : 5. Other Japanese records: Kobayashi, 1938*b* : 411; Kobayashi, 1941*e* : 513.
?phaselus tamurai Kobayashi, 1938*b* : 411.

DIAGNOSIS. Spermathecal pores paired, ventrolateral in furrows 5/6/7/8. Male pores superficial, on large porophores on segment 18. Genital markings absent. Intestinal caeca simple, often with incised ventral and dorsal margins, originating in segment 27.

JAPANESE RECORDS. **Hokkaido** (Hatai, 1930*b*; Kobayashi, 1941*b*); ISHIKAI (Ohfuchi, 1938); Sapporo (Hatai, 1930*b*; Yamaguchi, 1930*a*); OSHIMA Fukushima (Yamaguchi, 1962); Hachimano-cho in Hakodate, Kameda, Matsukage-cho in Hakodate & Ōma (Yamaguchi, 1962*a*); Hakodate (Kobayashi, 1938*b*); HIYAMA Imagane (Yamaguchi, 1962*a*). **Honshu** (**Ōu-Chihō**) (Kobayashi, 1941*b*); AOMORI-KEN Aomori, Kominato, Moura, Yokohama & Yuno-shima (Hatai, 1930*b*); MIYAGI-KEN Sendai (Hatai, 1930*b*): (**Kantō-Chihō**) (Kobayashi, 1941*b*); TŌKYŌ-TO Tokyo (Goto & Hatai, 1899): (**Chūbu-Chihō**) (Kobayashi, 1941*b*): (**Kinki-Chihō**) (Kobayashi, 1941*b*): (**Chūgoku-Chihō**) (Kobayashi, 1941*b*). **Shikoku** (Hatai, 1930*b*; Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b*); NAGASAKI-KEN Iki (Kobayashi, 1941*b*).

DISTRIBUTION. Japan and Korea.

Amynthas corticus (Kinberg, 1867)

corticus Kinberg, 1867 : 102.
diffringens Baird, 1869 : 40; (syn. *divergens, heterochaeta, heteropoda, indica, nipponica, oyamai, tajaroensis, ?torii*) Gates, 1972*c* : 18. Japanese records: Gates, 1938 : 209; Kobayashi, 1941*a* : 51, *b* : 261, *c* : 378, *d* : 458, *e* : 513.
indica Horst, 1883 : 186. Japanese records: Michaelsen, 1892 : 241.
heterochaeta Michaelsen, 1891*b* : 6. Japanese records: Ohfuchi, 1957 : 251.
?ijimae Rosa, 1891 : 402.
divergens Michaelsen, 1892 : 243. Other Japanese records: Ohfuchi, 1937*b* : 67; Ohfuchi, 1938*d* : 1993; Kobayashi, 1938*b* : 405; Kobayashi, 1941*b* : 260, *d* : 459, *e* : 513; Ohfuchi, 1941 : 252; Yamaguchi, 1962*a* : 5.
nipponica Beddard, 1892*b* : 760. Other Japanese records: Ohfuchi, 1937*b* : 109.
heteropoda Goto & Hatai, 1898 : 69. Other Japanese records: Ohfuchi, 1937*b* : 42, 138.
?marenzelleri Cognetti, 1906 : 780. Other Japanese records: Kobayashi, 1938*b* : 407; Yamaguchi, 1962*a* : 3.
oyamai Ohfuchi, 1937*b* : 62. Other Japanese records: Kobayashi, 1938*b* : 409; Yamaguchi, 1962*a* : 4.
tajiroensis Ohfuchi, 1938*b* : 46.
torii Ohfuchi, 1941 : 244.
?hatomajimensis Ohfuchi, 1957 : 245.

DIAGNOSIS. Spermathecal pores paired, about 0·3 body circumference apart, in furrows 5/6/7/8/9. Male pores superficial on small porophores on segment 18. Genital markings small numerous on pre and post clitellar segments. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. 'Japan' (Rosa, 1891; Michaelsen, 1892; Beddard, 1892). **Hokkaido** (Kobayashi, 1941*b*); ISHIKAI (Ohfuchi, 1938); OSHIMA, Hakodate and Nanayehama (Kobayashi, 1938*c*); Fukushima, Gobanzakai, Hachimano-cho & Matsukage-cho in Hakodate, Hakodate, Kameda, Ōma & Yakumo (Yamaguchi, 1962). **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b* & *c*); AKITA-KEN Ōdate (Ohfuchi, 1937*b*); IWATE-KEN Morioka (Ohfuchi, 1937*b*); YAMAGATA-KEN Fukuura & Nezugaseki (Ohfuchi, 1937*b*); MIYAGI-KEN Sendai, Tajiri and Tō-katta (Ohfuchi, 1937*b*); FUKUSHIMA-KEN Inawashiro, Kaneyama, Kitakata, Mikami, Taira, Tanagura, Tokusawa, Wakamatsu, Yashiro & Yashirogawa (Ohfuchi, 1937*b*): (**Kantō-Chihō**) (Kobayashi, 1941*b*); TOCHII-KEN Utsunomiya (Kobayashi, 1941*d*); IBARAKI-KEN Hirakata (Ohfuchi, 1937*a*) Mito (Ohfuchi, 1937*b*); SAITAMA-KEN Tokorozawa (Goto & Hatai, 1898); TŌKYŌ-TO Komaba (Ohfuchi, 1937*b*); Tokyo (Goto & Hatai, 1898; Gates, 1938); KANAGAWA-KEN Izumitzu on Ō-shima & Odawara (Ohfuchi, 1937*b*);

Kamakura (Goto & Hatai, 1898); Ō-shima (Kobayashi, 1941b & c); Yokohama (Cognetti, 1906): **(Chūbu-Chihō)** (Kobayashi, 1941b & c); SHIZUOKA-KEN Hamana Kō (Ohfuchi, 1937b): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c; SHIMANE-KEN Oki-guntō (Kobayashi, 1941a & b). **Shikoku** (Kobayashi, 1941b & c); EHIME-KEN Matsuyama (Ohfuchi, 1937b); KOCHI-KEN Kōchi (Ohfuchi, 1937b); Mt Sampōzan (Ohfuchi, 1941). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b, c & e); NAGASAKI-KEN Gottō-rettō and Iki (Kobayashi, 1941b); ŌITA-KEN Kawanabori (Ohfuchi, 1941); KUMAMOTO-KEN Izumi (Ohfuchi, 1937b); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941c); Tomitaka (Ohfuchi, 1937b); KAGOSHIMA-KEN Ibuki, Kirishima Yama & Kagoshima (Ohfuchi, 1937b); Kagoshima, Kaimon-dake, Shibushi & Yanakawa (Kobayashi, 1941c). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941b & c). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941b & c); Onna (Ohfuchi, 1957). **Sakishima-Guntō** IRIOMOTE-JIMA Hatoma-jima (Ohfuchi, 1957).

DISTRIBUTION. Indigenous range uncertain. Introduced by man into many parts of the world (for details see Gates, 1972a : 177 as *diffringens*).

Amynthas flavescens (Goto & Hatai, 1898)

flavescens Goto & Hatai, 1898 : 72.
?producta Goto & Hatai, 1898 : 73.
?houletti bidenryoana Ohfuchi, 1956 : 169.
?leucocirca: Ohfuchi, 1956 : 174 [*?non* Chen, 1933 : 262].
?noharuzakiensis Ohfuchi, 1956 : 175.

DIAGNOSIS. Spermathecal pores paired in furrows 6/7/8/9. Male pores superficial on segment 18. Genital markings, serial, in line with spermathecal pores on segments 7–9; in clusters near male pores on segment 18. Intestinal caeca simple with smooth dorsal and ventral margins, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** TŌKYŌ-TO Tokyo (Goto & Hatai, 1898). **Sakishima-Guntō** ISHIGAKI-SHIMA Nobaru-zaki (Ohfuchi, 1956); IRIOMOTE-JIMA Hatoma-jima & Sonai (Ohfuchi, 1956).

DISTRIBUTION. Japan.

Amynthas glabrus (Gates, 1932)

glabra Gates, 1932 : 395; (syn. *vieta*) Gates, 1972a : 187.
vieta Gates, 1936 : 462. Japanese records: Kobayashi, 1941c : 378, e : 513.
?papillio: Ohfuchi, 1956 : 140 [non Gates, 1930 : 316].

DIAGNOSIS. Spermathecal pores paired, postsetal on segment 6. Male pores superficial on segment 18 with seminal grooves to paired porophores on segments 17–18. Genital markings absent. Intestinal caeca sample with smooth margins originating in segment 27.

JAPANESE RECORDS. **Kyushu** (Kobayashi, 1941e). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941c). **Sakishima-Guntō** IRIOMOTE-JIMA Hoshitate (Ohfuchi, 1956).

DISTRIBUTION. Burma and Japan.

Amynthas gracilis (Kinberg, 1867)

gracilis Kinberg, 1867 : 112.
hawayana Rosa, 1891 : 396. Japanese records: Kobayashi, 1941c : 378, e : 513; Ohfuchi, 1956 : 166.
?kamakurensis Goto & Hatai, 1898 : 68.
?parvula Goto & Hatai, 1898 : 68 [non Ohfuchi, 1956 (= *Metaphire parvula*)].
?decimpapillata Goto & Hatai, 1898 : 71.
?carnosa Goto & Hatai, 1899 : 15. Japanese records: Ohfuchi, 1937b : 56; Kobayashi, 1941b : 260; Yamaguchi, 1962a : 1.
?kagoshimensis Takahashi, 1932 : 343.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·30 body circumference apart in furrows 5/6/7/8. Male pores superficial on small porophore on segment 18. Genital markings small, clusters of up to 11 papillae median to the male pores on segment 18 and occasionally 17 and 19; paired median to the spermathecal pores on segments 5–8. Intestinal caeca simple with incised margins, originating in segment 27.

JAPANESE RECORDS. **Hokkaido** (Kobayashi, 1941*b*) OSHIMA Ōma (Yamaguchi, 1962). **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b*); IWATE-KEN Kuji & Morioka (Ohfuchi, 1937*b*); YAMAGATA-KEN Sakata & Tobi-shima (Ohfuchi, 1937*b*); MIYAGI-KEN Wakuga (Ohfuchi, 1937*b*): **(Kantō-Chihō)** (Kobayashi, 1941*b*); TŌKYŌ-TO Tokyo (Goto & Hatai, 1898, 1899); KANAGAWA-KEN Kamakura (Goto & Hatai, 1898); O-shima (Kobayashi, 1941*c*): **(Chūbu-Chihō)** (Kobayashi, 1941*b*): **(Kinki-Chihō)** (Kobayashi, 1941*b*). **Shikoku** (Kobayashi, 1941*b*); EHIME-KEN Matsuyama (Ohfuchi, 1937*b*). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*c* & *e*); NAGASAKI-KEN Gottō-rettō (Kobayashi, 1941*b*); KAGOSHIMA-KEN Kagoshima, Shibushi & Yanakawa (Kobayashi, 1941*c*). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941*c*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*c*); Onna (Ohfuchi, 1956).

DISTRIBUTION. Indigenous range uncertain. Introduced by man into many parts of the world (for details see Gates, 1972*a* : 189 as *hawayanus*).

Amynthas habereri (Cognetti, 1906)

habereri Cognetti, 1906 : 777.

DIAGNOSIS. Spermathecal pores closely paired in furrows 5/6/7/8/9. Male pores superficial on large porophores on segment 18. Genital markings small, paired, pre and postsetal, in line with the male pores on segments 19 and 20. Intestinal caeca manicate each with about 10 diverticula originating in segment 26.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** KANAGAWA-KEN, Yokohama (Cognetti, 1906).

DISTRIBUTION. Japan only.

Amynthas hilgendorfi species-complex

INCLUDED SPECIES
hilgendorfi Michaelsen, 1892 : 235; (syn. *rokugo, irregularis, schizopora*) Beddard, 1900 : 633. Other Japanese records: Michaelsen, 1899 : 9; Michaelsen, 1916 : 11; Michaelsen, 1923 : 237; Yamaguchi, 1930*a* : 50; 1930*b* : 89; Kobayashi, 1938*b* : 407; Ohfuchi, 1938*d* : 1994; Kobayashi, 1941*a* : 51, *b* : 260, *c* : 378, *d* : 459, *e* : 513; Yamaguchi, 1962*a* : 14; Nakamura, 1967 : 164; Tamura et al, 1969 : 26.
rokugo Beddard, 1892*b* : 756.
tokioensis Beddard, 1892*b* : 762.
sieboldi: Beddard, 1892*b* : 759; Goto & Hatai, 1898 : 65 [non Horst, 1883 (= *Metaphire sieboldi*)].
vittata Goto & Hatai, 1898 : 74. Other Japanese records: Cognetti, 1906 : 783; Hatai, 1929 : 271; Kobayashi, 1941*b* : 260, *c* : 378, *d* : 459, *e* : 513; Yamaguchi, 1962*a* : 16.
schizopora Goto & Hatai, 1898 : 76.
irregularis Goto & Hatai, 1899 : 13. Other Japanese records: Ohfuchi, 1938*a* : 1; Ohfuchi, 1939*a* : 81; Kobayashi, 1941*a* : 51, *b* : 260, *c* : 378, *d* : 459, *e* : 513; Yamaguchi, 1962*a* : 17.
agrestis Goto & Hatai, 1899 : 17. Other Japanese records: Hatai, 1930*b* : 651; Yamaguchi, 1930*a* : 51; Kobayashi, 1938*b* : 405; Kobayashi, 1941*a* : 51, *b* : 260, *c* : 378, *e* : 513; Yamaguchi, 1962*a* : 13; Nakamura, 1967 : 164.
glandularis Goto & Hatai, 1899 : 18. Other Japanese records: Kobayashi, 1941*b* : 260.
levis Goto & Hatai, 1899 : 20.
communissima (syn. *sieboldi*: Goto & Hatai, 1898) Goto & Hatai, 1899 : 23. Other Japanese records: Ohfuchi, 1938*d* : 1994; Kobayashi, 1941*b* : 260; Takahashi & Yamaguchi, 1961 : 1; Yamaguchi, 1962*a* : 13.
sieboldi lenzi Michaelsen, 1899 : 9.
ambigua Cognetti, 1906 : 782.

yunoshimensis Hatai, 1930*b* : 655. Other Japanese records: Kobayashi, 1941*b* : 260; Tamura et al, 1969 : 26.

tappensis Ohfuchi, 1935 : 409. Other Japanese records: Kobayashi, 1941*b* : 260.

gomejimensis Ohfuchi, 1937*a* : 18. Other Japanese records: Kobayashi, 1941*b* : 260, *c* : 378, *e* : 513.

Members of the hilgendorfi species-complex not recorded from Japan
gucheoensis Song & Paik, 1970.
jiriensis Song & Paik, 1971.
koreana Kobayashi, 1938*a*.
shinkeiensis Kobayashi, 1938*a*.

DIAGNOSIS. Spermathecal pores absent or paired, ventrolateral in furrows 5/6/7/8 or 6/7/8 or 6/7 or 7/8. Male pores absent or superficial. Large clusters of genital markings or indistinct pigmented areas on pre- and postclitellar segments. Intestinal caeca manicate, each with about 5 diverticula, originating in segment 27.

REMARKS. Nineteen species and subspecies are included within the *hilgendorfi* species-complex, they exhibit a wide range of variation in the expression of several characters, especially in the arrangement of genital markings, number of spermathecal furrows and the degree of development of the male pores. Insufficient data are currently available either to establish the validity of the component taxa or to recognize discrete subgroups within the complex.

JAPANESE RECORDS. 'Japan' (Beddard, 1892; Michaelsen, 1892). **Hokkaido** (Kobayashi, 1941*b* & *c*); ISHIKAI (Ohfuchi, 1938); Sapporo (Hatai, 1930*b*; Yamaguchi, 1930*a* & *b*; Nakamura, 1967); HIDAKA Hidaka-Mombetsu (Tamura et al, 1969); OSHIMA Hakodate (Michaelsen, 1892; Kobayashi, 1938*c*); Hachimano-cho in Hakodate & Fukushima (Takahashi & Yamaguchi, 1961; Yamaguchi, 1962); Gobanzakai, Mt. Hakodate, Kameda, Matsukage-cho in Hakodate, Ōno, Ōma, Yakumo & Yunokawa-cho (Yamaguchi, 1962); HIYAMA Imagane (Yamaguchi, 1962). **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b* & *c*); AOMORI-KEN (Hatai, 1930*b*); Goshogawara (Ohfuchi, 1938*a*, 1939*a*); Kamome-jima (Ohfuchi, 1937*a*); Kominato (Hatai, 1929); Tappi (Ohfuchi, 1935); Tsugaru (Goto & Hatai, 1898, 1899); Yunoshima (Hatai, 1929, 1930); Asamushi, Fukaura, Hachinohe, Hamana, Imabetsu, Kanita, Kodomani, Mimmaya, Nakasato, Nishimeya, Nobeji, Oma, Sai, Sambongi, Shimofuro, Tanabu, & Yokohama (Ohfuchi, 1939*a*); AKITA-KEN Ōyu (Ohfuchi, 1938*a*, 1939*a*); Arase, Komagadake, Omagari, Takanosu & Tsuchizaki-minato (Ohfuchi, 1939*a*); IWATE-KEN (Hatai, 1930*b*); Orikabe (Ohfuchi, 1938*a*, 1939*a*); Funakoshi, Hanamaki, Kawashiri, Kuji, Kurosawijira, Miyako, Morioka, Ofunato, & Zuizan (Ohfuchi, 1939*a*); YAMAGATA-KEN Goshiki and Sakata (Ohfuchi, 1938*a*, 1939*a*); Arato, Higashine, Hondōji, Kogane, Tobi-shima & Tsuruoka (Ohfuchi, 1939*a*); MIYAGI-KEN Nakayamadaira (Ohfuchi, 1938*a*, 1939*a*); Miyagi (Hatai, 1930*b*); Sendai (Goto & Hatai, 1898, 1899, Hatai, 1929, 1930, Ohfuchi, 1939*a*); Yoshidahama (Ohfuchi, 1938*a*); Aone, Ayashi, Eno-shima, Hamayoshida, Ishinomaki, Kesennuma, Kinka-zan, Maeyachi, Okawara, Ō-shima, Shiroishi, Tō-katta & Wakuga (Ohfuchi, 1939*a*); FUKUSHIMA-KEN Aizu province (Kobayashi, 1936 *f*); Kaneyama, Tadami & Yamaguchi (Ohfuchi, 1938*a*, 1939*a*); Yashiro (Ohfuchi, 1938*a*); Azuma-fuji, Nakamura, Shirakawa, Tajima, Tanagura, Tokusawa & Wakamatsu (Ohfuchi, 1939*a*): **(Kantō-Chihō)** (Kobayashi, 1941*b*); TOCHII-KEN Utsunomiya (Kobayashi, 1941*d*); IBARAKI-KEN (Goto & Hatai, 1899); Ōarami (Goto & Hatai, 1899, Hatai, 1930*b*); SAITAMA-KEN Tokorozawa (Goto & Hatai, 1899, Hatai, 1930*b*); TŌKYŌ-TO, Tokyo (Goto & Hatai, 1898, 1899); KANAGAWA-KEN Kamakura (Goto & Hatai, 1898); Misaki (Michaelsen, 1923); Ō-Shima (Hatai, 1929, 1930*b*); Yokohama (Michaelsen, 1892, Cognetti, 1906): **(Chūbu-Chihō)** (Kobayashi, 1941*b*, *c*); YAMANASHI-KEN Fiji-san (Michaelsen, 1916); SHIZUOKA-KEN (Goto & Hatai, 1898, 1899): **(Kinki-Chihō)** (Kobayashi, 1941*b*, *c*); HYOGO-KEN Nakahama (Michaelsen, 1899): **(Chūgoku-Chihō)** (Kobayashi, 1941*b*, *c*); SHIMANE-KEN Oki-guntō (Kobayashi, 1941*a*, *b*); OKAYAMA-KEN Bitiu district & Takahashi (Goto & Hatai, 1899). **Shikoku** (Kobayashi, 1941*b*, *c*); EHIME-KEN Matsugama (Hatai, 1930*b*); Unajima

(Goto & Hatai, 1899, Michaelsen, 1916, Hatai, 1929). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b, c, e*); NAGASAKI-KEN Iki (Kobayashi, 1941*b*); KUMAMOTO-KEN Kumamoto (Goto & Hatai, 1899); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941*c*), Tomitaka (Hatai, 1930*b*); KAGOSHIMA-KEN Kagoshima (Hatai, 1930*b*, Kobayashi, 1941*c*); Kirishima Yama (Hatai, 1929, Kobayashi, 1941*c*); Sakura-jima (Hatai, 1929); Kaimon-dake, Shibushi, & Yanakawa (Kobayashi, 1941*c*). **Osumi-Guntō** Yaku-shima (Kobayashi, 1941*b, c*).

DISTRIBUTION. Japan and Korea, two taxa, *hilgendorfi* and *levis,* introduced into North America.

Amynthas hupiensis (Michaelsen, 1895)

hupiensis Michaelsen, 1895 : 35. Japanese records: Michaelsen, 1899 : 6; Ohfuchi, 1938*d* : 1993; Kobayashi, 1941*b* : 260, *c* : 378, *d* : 459, *e* : 513; Yamaguchi, 1962*a* : 9; Nakamura, 1967 : 164.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·16 body circumference apart in furrows 6/7/8/9. Male pores superficial on small porophore on segment 18. Genital markings large paired intersegmental in line with the male pores at 17/18 and 18/19. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. **Hokkaido** ISHIKAI (Ohfuchi, 1938*d*); Sapporo (Nakamura, 1967); OSHIMA Hachimano-cho & Maksukage-cho in Hakodate & Ono (Yamaguchi, 1962). **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b* & *c*): **(Kantō-Chihō)** (Kobayashi, 1941*b*); TOCHII-KEN Utsunomiya (Kobayashi, 1941*d*): **(Chūbu-Chihō)** (Kobayashi, 1941*b* & *c*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*); HYOGO-KEN Nakahama (Michaelsen, 1899): **(Chūgoku-Chihō)** (Kobayashi, 1941*b* & *c*). **Shikoku** (Kobayashi, 1941*b* & *c*). **Kyushu** (Kobayashi, 1941*b, c* & *e*); NAGASAKI-KEN Iki (Kobayashi, 1941*b*); KAGOSHIMA-KEN Kagoshima & Shibushi (Kobayashi, 1941*c*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*b* & *c*).

DISTRIBUTION. China and Japan, introduced into North America and New Zealand.

Amynthas illotus species-group

illotus species-group Sims & Easton, 1972 : 236.

DIAGNOSIS. Spermathecal pores absent. Male pores superficial. Intestinal caeca simple, originating in or near segment 27.

REMARKS. This species-group was recognized by Sims & Easton (1972) to accommodate several poorly described species which lack spermathecal pores. These species do not have any special affinities with one another, instead the group is one of convenience. It is highly probable that when more data become available most of the included species will be found to be synonymous with other thecate species. Two species have been recorded from Japan: *A. illotus* and *A. pusillus.*

For convenience the athecate species *'Pheretima' oyuensis* Ohfuchi, 1956 is also considered here although it is not a member of the *illotus* species-group. This species was considered *incertae sedis* by Sims & Easton (1972) since it lacks male pores, the structure of which are diagnostic of the caecate genera *Amynthas, Metaphire* and *Pheretima.*

Amynthas 'illotus' (Gates, 1932)

illota: Ohfuchi, 1956 : 136 (*non* Gates, 1932 : 397).

DIAGNOSIS. Length 125–155 mm, 125–144 segments. Genital markings absent. 109–114 setae on segment *vii.*

REMARKS. The diagnosis of *A. illotus* was restricted by Gates (1972*a* : 196) to exclude the Japanese specimens identified by Ohfuchi. They cannot be assigned to another species but it is not proposed to recognize a new species to accommodate them since it is probable that

when more data become available, they will be found to belong to a previously described species.

JAPANESE RECORDS. **Sakishima-Guntō** ISHIGAKI-SHIMA Ibaruma (Ohfuchi, 1956); IRIOMOTE-JIMA Hatoma-jima & Hoshitate (Ohfuchi, 1956).

DISTRIBUTION. Japan.

Amynthas pusillus (Ohfuchi, 1956)

pusilla Ohfuchi, 1956 : 136 [*non* Ude, 1893 : 63 (= *Amynthas minimus*)].

DIAGNOSIS. Length 44–50 mm, 75–93 segments. Genital markings absent. 33–37 setae on *vii*.

JAPANESE RECORDS. **Sakishima-Guntō** IRIOMOTE-JIMA Sonai (Ohfuchi, 1956).

DISTRIBUTION. Japan.

'Pheretima' oyuensis Ohfuchi, 1937

oyuensis Ohfuchi, 1937a : 24.

DIAGNOSIS. Length 50–55 mm, 87–94 segments. Male pores and prostates absent. Genital markings absent. *C.* 38 setae on *vii*.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** AKITA-KEN Inariyama, Oyu Katstuno district (Ohfuchi, 1937).

DISTRIBUTION. Japan.

Amynthas japonicus (Horst, 1883)

japonica Horst, 1883 : 192.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·43 body circumference apart in furrows 6/7/8. Male pores superficial on segment 18 in seminal grooves which extend onto segment 17. Genital markings absent. Intestinal caeca manicate, each with about 8 diverticula, originating in segment 26.

JAPANESE RECORDS. 'Japan' (Horst, 1883).

DISTRIBUTION. Japan.

Amynthas megascolidioides (Goto & Hatai, 1899)

megascolidioides Goto & Hatai, 1899 : 21. Other Japanese records: Kobayashi, 1941a : 51, b : 260.

DIAGNOSIS. Spermathecal pores paired, in furrows 4/5/6/7/8/9. Male pores superficial on segment 19. Genital markings small, paired, postsetal in line with the male pores on segments 17, 18 and 20. Intestinal caeca simple, originating in segment 27.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** (Kobayashi, 1941b): **(Kantō-Chihō)** TŌKYŌ-TO Tokyo (Goto & Hatai, 1899): **(Chūbu-Chihō)** (Kobayahi, 1941b): **(Kinki-Chihō)** (Kobayashi, 1941b): **(Chūgoku-Chihō)** (Kobayashi, 1941b); SHIMANE-KEN Oki-guntō (Kobayashi, 1941a & b). **Shikoku** (Kobayashi, 1941b). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b).

DISTRIBUTION. Korea and Japan.

Amynthas micronarius (Goto & Hatai, 1898)

micronaria Goto & Hatai, 1898 : 74. Other Japanese records: Ohfuchi, 1937b : 50; Kobayashi, 1941b : 260, c : 378, d : 459, e : 513; Yamaguchi, 1962a : 8.
?*shimaensis* Goto & Hatai, 1899 : 15. Other Japanese records: Kobayashi, 1941b : 260.

?yamizoyamensis Ohfuchi, 1935 : 413. Other Japanese records: Ohfuchi, 1937*b* : 133.
?obtusa Ohfuchi, 1957 : 244.

DIAGNOSIS. Spermathecal pores paired, *c*. 0·30 body circumference apart in furrows 5/6/7/8/9. Male pores superficial on small porophores on segment 18. Genital markings large paired, intersegmental in furrows 17/18, 18/19 and occasionally 19/20. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. **Hokkaido** OSHIMA Hachimano-cho in Hakodate (Yamaguchi, 1962). **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b* & *c*); MIYAGI-KEN Sendai (Ohfuchi, 1937*b*); FUKUSHIMA-KEN Yamizo-san (Ohfuchi, 1937*b*): **(Kantō-Chihō)** (Kobayashi, 1941*b*); GUMMA-KEN Shima (Goto & Hatai, 1899); TOCHII-KEN Utsunomiya (Kobayashi, 1941*d*); TŌKYŌ-TO Tokyo (Goto & Hatai, 1898): **(Chūbu-Chihō)** (Kobayashi, 1941*b* & *c*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*): **(Chūgoku-Chihō)** (Kobayashi, 1941*b* & *c*). **Shikoku** (Kobayashi, 1941*b* & *c).* **Kyushu** (Kobayashi, 1941*b, c* & *d*); NAGASAKI-KEN Gottō-rettō (Kobayashi, 1941*b*); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941*c*). **Sakishima-Guntō** IRIOMOTE-JIMA Sonai (Ohfuchi, 1957).

DISTRIBUTION. Japan.

Amynthas minimus (Horst, 1893)

minimus Horst, 1893 : 66.
zoysiae Chen, 1933 : 288. Japanese records: Kobayashi, 1941*c* : 378, *e* : 513.
ishikawai Ohfuchi, 1941 : 248. Other Japanese records: Kobayashi, 1941*b* : 260.

DIAGNOSIS. Spermathecal pores paired, *c*. 0·52 body circumference apart in furrow 5/6 only. Male pores superficial on small porophores on segment 18. Genital markings small on pre and postclitellar segments. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** KANAGAWA-KEN Ō-shima (Kobayashi, 1941*c*). **Shikoku** (Kobayashi, 1941*b*); KŌCHI-KEN Mt Sampōzan (Ohfuchi, 1941). **Kyushu** (Kobayashi, 1941*c* & *e*); KAGOSHIMA-KEN Yanakawa (Kobayashi, 1941*c*). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941*c*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*c*).

DISTRIBUTION. Indigenous range uncertain. Introduced by man into many parts of the world (for details see Gates, 1972*a* : 201).

Amynthas morrisi (Beddard, 1892)

morrisi Beddard, 1892*a* : 166. Japanese records: Kobayashi, 1941*c* : 378, *e* : 513; Ohfuchi, 1956 : 143.
elongata: Ohfuchi, 1956 : 148 [non Perrier, 1872 : 124 (=*Polypheretima elongata*)].
exiloides: Ohfuchi, 1956 : 142 (non Chen, 1936 : 288).

DIAGNOSIS. Spermathecal pores paired, *c*. 0·50 body circumference apart in furrows 5/6/7. Male pores superficial on small porophores on segment 18. Genital markings small, slightly median to spermathecal pores; single median on segments 6–8; in transverse rows of up to 4, pre- and postsetal on postclitellar segments and 1 or 2 closely associated with the male pores. Intestinal caeca, simple with an incised ventral margin, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** KANAGAWA-KEN Ō-shima (Kobayashi, 1941*c*). **Kyushu** (Kobayashi, 1941*c* & *e*) KAGOSHIMA-KEN Shibushi (Kobayashi, 1941*c*). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941*c*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*c*) Higaki near Onna (Ohfuchi, 1956). **Sakishima-Guntō** ISHIGAKI-SHIMA (Ohfuchi, 1956); IRIOMOTE-JIMA Obama-jima & Sonai (Ohfuchi, 1956).

DISTRIBUTION. Indigenous range uncertain. Introduced by man into many parts of the world (for details see Gates, 1972*a* : 202).

Amynthas obscurus (Goto & Hatai, 1898)

obscura Goto & Hatai, 1898 : 70.

DIAGNOSIS. Spermathecal pores paired, postsetal on segments 6, 7 and 8. Male pores superficial on segment 18. Genital markings median to male pores, pre- and postsetal on segment 18, postsetal on segment 19. Intestinal caeca simple, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** KANAGAWA-KEN Kamakura (Goto & Hatai, 1898).

DISTRIBUTION. Japan.

Amynthas papulosus (Rosa, 1896)

papulosa Rosa, 1896 : 525; (syn. *papulosa sauteri, ?rockefelleri*) Gates, 1972a : 206.
papulosa sauteri Michaelsen, 1922 : 26. Japanese records: Ohfuchi, 1956 : 164.
rockefelleri Chen, 1933 : 238. Japanese records: Kobayashi, 1941c : 378, e : 513.

DIAGNOSIS. Spermathecal pores paired, c. 0·25 body circumference apart in furrows 5/6/7/8. Male pores superficial on small porophores on segment 18. Genital markings small, numerous, in pre- and postsetal rows on segments 6–9 and 17–19. Intestinal caeca simple with smooth margins, originating in segment 27.

REMARKS. This species may be confused with *A. gracilis* from which it differs only in its different arrangement of genital markings and smaller size (*papulosus* = 45–78 mm; *gracilis* = 56–156 mm).

JAPANESE RECORDS. **Kyushu** (Kobayashi, 1941e). **Osumi-Guntō** YAKU-SHIMA (Kobayashi, 1941c). **Sakishima-Guntō** ISHIGAKI-SHIMA (Ohfuchi, 1956); IRIOMOTE-JIMA Hoshitate & Sonaidake (Ohfuchi, 1956).

DISTRIBUTION. Japan, China, Taiwan, Burma, Thailand, Sumatra.

Amynthas parvicystis (Goto & Hatai, 1899)

parvicystis Goto & Hatai, 1899 : 18. Other Japanese records: Kobayashi, 1941b : 260.

DIAGNOSIS. Spermathecal pores paired, presetal on segments 7 and 8. Male pores superficial on small porophores on segment 18. Genital markings small in the intersegmental furrows in front of the spermathecal pores and median to the male pores on 18. Intestinal caeca simple with an incised ventral and dorsal margins, originating in segment 26.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** IBARAKI-KEN Ōarami (Goto & Hatai, 1899). **Shikoku** (Kobayashi, 1941b); EHIME-KEN Uwajima (Goto & Hatai, 1899).

DISTRIBUTION. Japan.

Amynthas robustus (Perrier, 1872)

robusta Perrier, 1872 : 112; (syn. *campestris, corrugata, lauta, mastakae*) Ljungstöm, 1971 : 27. Japanese records: Kobayashi, 1941b : 261; c : 378; e : 513.
mastakae Beddard, 1892b : 761. Japanese records: Ohfuchi, 1938c : 62; Kobayashi, 1941b : 260, e : 513.
campestris Goto & Hatai, 1898 : 67 [non Lee, 1952 : 39 (= *Amynthas corticus*)].
lauta Ude, 1905 : 405. Japanese records: Ohfuchi, 1956 : 155.
corrugata Chen, 1931 : 131. Japanese records: Ohfuchi, 1956 : 162.

DIAGNOSIS. Spermathecal pores paired, c. 0·50 body circumference apart in furrows 7/8/9. Male pores superficial on small, paired porophores on segment 18. Genital markings small, numerous on segments 7, 8 and 18. Intestinal caeca simple with incised ventral margins, originating in segment 27.

JAPANESE RECORDS. 'Japan' (Beddard, 1892). **Honshu (Kantō-Chihō)** KANAGAWA-KEN Kamakura (Goto & Hatai, 1898); Ō-shima (Kobayashi, 1941*b* & *c*): **(Chūbu-Chihō)** (Kobayashi, 1941*b*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*): WAKAYAMA-KEN Gobō Machi (Ohfuchi, 1938*c*). **Shikoku** (Kobayashi, 1941*b* & *c*); KŌCHI-KEN Mt Sampōzan (Ohfuchi, 1941). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b, c* & *e*); NAGASAKI-KEN Gottō-rettō (Kobayashi, 1941*b*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*b* & *c*); Onna & Shiragaki (Ohfuchi, 1956). **Sakishima-Guntō** ISHIGAKI-SHIMA (Ohfuchi, 1956).

DISTRIBUTION. Indigenous range uncertain. Introduced into many parts of the world by man (for details see Ljungstöm, 1971 : 27).

Amynthas scholasticus (Goto & Hatai, 1898)

scholastica Goto & Hatai, 1898 : 70.

DIAGNOSIS. Spermathecal pores paired, in furrows 4/5/6/7/8. Male pores superficial on segment 18. Genital markings absent. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** TŌKYŌ-TO Tokyo (Goto & Hatai, 1898).

DISTRIBUTION. Japan.

Metaphire californica (Kinberg, 1867)

californica Kinberg, 1867 : 102. Japanese records: Kobayashi, 1941*b* : 260, *c* : 378, *e* : 513; Ohfuchi, 1956 : 158.
?sakaguchii Ohfuchi, 1938*c* : 53. Japanese records: Ohfuchi, 1941 : 252.
?sonaiensis Ohfuchi, 1956 : 154.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·50 body circumference apart in furrows 7/8/9. Male pores within copulatory pouches on segment 18. Genital markings absent. Intestinal caeca simple often with incised dorsal and ventral margins, originating in segment 27.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** KANAGAWA-KEN Ō-shima (Kobayashi, 1941*b* & *c*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*); WAKAYAMA-KEN Gobō Machi (Ohfuchi, 1938*c*): **(Chūgoku-Chihō)** (Kobayashi, 1941*b* & *c*). **Shikoku** (Kobayashi, 1941*b* & *c*); KŌCHI-KEN Mt Sampōzan & Nishibun-mura (Ohfuchi, 1938*c*). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b, c* & *e*); NAGASAKI-KEN Gottō-rettō & Iki (Kobayashi, 1941*b*); KAGOSHIMA-KEN Kagoshima & Yanakawa (Kobayashi, 1941*c*). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941*b* & *c*); Shiragaki (Ohfuchi, 1956). **Sakishima-Guntō** IRIOMOTE-JIMA Sonai (Ohfuchi, 1956).

DISTRIBUTION. Indigenous range uncertain. Introduced by man into many parts of the world (for details see Gates, 1972*a* : 174).

Metaphire fuscata (Goto & Hatai, 1898)

fuscata Goto & Hatai, 1898 : 66.
?grossa Goto & Hatai, 1898 : 75. Other Japanese records: Ohfuchi, 1937*b* : 33; Kobayashi, 1941*b* : 260.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·20 body circumference apart in furrows 5/6/7/8/9. Spermathecal diverticula convoluted. Male pores within copulatory pouches on segment 18. Genital markings paired, postsetal, slightly median to the male pores on segments 17–22, sometimes slightly median to the spermathecal pores on segments 5–8. Intestinal caeca simple with incised dorsal and ventral margins, originating in segment 27.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** (Kobayashi, 1941*b*); MIYAGI-KEN Yagiyama in Sendai (Ohfuchi, 1937*b*); FUKUSHIMA-KEN Yamizo-san (Ohfuchi, 1937*b*): **(Kantō-Chihō)**

(Kobayashi, 1941*b*); KANAGAWA-KEN Kamakura (Goto & Hatai, 1898): **(Chūhu-Chihō)** (Kobayashi, 1941*b*); YAMANASHI-KEN Kawaguchi (Goto & Hatai, 1898).

DISTRIBUTION. Japan.

Metaphire hataii (Ohfuchi, 1937)

hataii Ohfuchi, 1937*a* : 13.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·37 body circumference apart in furrows 5/6/7/8. Male pores within copulatory pouches on segment 18. Genital markings large, paired on segments 7 and 18. Intestinal caeca manicate, each with 6 diverticula, originating in segment 27.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** IWATE-KEN Kyū-sakurayama near Morioka (Ohfuchi, 1937*a*).

DISTRIBUTION. Japan.

Metaphire parvula (Ohfuchi, 1956)

parvula Ohfuchi, 1956 : 152 [non Goto & Hatai, 1898 : 68 (= *Amynthas gracilis*)].

DIAGNOSIS. Spermathecal pores paired, ventrolateral in furrows 6/7/8. Male pores within copulatory pouches on segment 18. Genital markings absent. Intestinal caeca simple with smooth margins, originating in segment 27.

JAPANESE RECORDS. **Sakishima-Guntō** IRIOMOTE-JIMA Sonai (Ohfuchi, 1956).

DISTRIBUTION. Japan.

Metaphire peguana (Rosa, 1890)

peguana Rosa, 1890 : 113. Japanese records: Ohfuchi, 1956 : 171.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·28 body circumference apart in furrows 6/7/8/9. Male pores within copulatory pouches on segment 18. Genital markings large, paired, inter-segmental in furrows 17/18 and 18/19. Intestinal caeca simple with smooth margins, originating in segment 27.

REMARKS. Gates (1972*a*) was of the opinion that Ohfuchi's record cannot be accommodated within this species but he did not indicate to which species it could be assigned.

JAPANESE RECORDS. **Sakishima-Guntō** ISHIGAKI-SHIMA Ibaruma (Ohfuchi, 1956).

DISTRIBUTION. Burma, Thailand, Vietnam, Malaya, Java, Borneo and Japan.

Metaphire riukiuensis (Ohfuchi, 1957)

riukiuensis Ohfuchi, 1957 : 248.

DIAGNOSIS. Spermathecal pores paired in furrows 5/6/7/8/9. Male pores within copulatory pouches the openings of which occupy segments 17, 18 and 19. (or ? in seminal grooves). Genital markings absent. Intestinal caeca simple with incised ventral margins, originating in segment 27.

JAPANESE RECORDS. **Sakishima-Guntō** MIYAKO-JIMA (Ohfuchi, 1957); ISHIGAKI-SHIMA (Ohfuchi, 1957); IRIOMOTE-JIMA Hatoma-jima, Hoshitate & Sonai (Ohfuchi, 1957).

DISTRIBUTION. Japan.

Metaphire schmardae (Horst, 1883)

schmardae Horst, 1883 : 194. Other Japanese records: Michaelsen, 1892 : 235; Kobayashi, 1941*b* : 261, *c* : 378, *e* : 513.
kikuchii Hatai & Ohfuchi, 1936 : 767.

DIAGNOSIS. Spermathecal pores paired, ventrolateral in furrows 7/8/9. Male pores within copulatory pouches on segment 18. Genital markings absent. Intestinal caeca manicate, each with 5 diverticula, originating in segment 27.

JAPANESE RECORDS. 'Japan' (Horst, 1883; Michaelsen, 1892). **Honshu (Ōu-Chihō)** FUKUSHIMA-KEN Nakamura (Hatai & Ohfuchi, 1936): **(Kantō-Chihō)** (Kobayashi, 1941b); IBARAKI-KEN Hirakata, Mito & Onuka (Hatai & Ohfuchi, 1936); KANAGAWA-KEN Ō-shima (Kobayashi, 1941b & c): **(Chūbu-Chihō)** (Kobayashi, 1941b & c): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c). **Shikoku** (Kobayashi, 1941b & c). **Tsushima** (Kobayashi, 1941b). **Kyushu** (Kobayashi, 1941b, c & e); NAGASAKI-KEN Gottō-rettō & Iki (Kobayashi, 1941b); KAGOSHIMA-KEN Kagoshima & Shibushi (Kobayashi, 1941c). **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941b & c).

DISTRIBUTION. Japan, China, Taiwan. Also introduced by man into several countries outside of the *Pheretima* domain.

Metaphire servina (Hatai & Ohfuchi, 1937)

servina Hatai & Ohfuchi, 1937 : 1.

DIAGNOSIS. Spermathecal pores paired, c. 0·50 body circumference apart in furrows 6/7/8/9. Spermathecal diverticula present. Male pores in copulatory pouches behind the setal line on segment 18. Secretory diverticula absent. Genital markings small, paired, median to the male pores on segment 18. Intestinal caeca manicate each with 6 diverticula, originating in segment 27.

JAPANESE RECORDS. **Honshu (Ōu-Chihō)** AOMORI-KEN Asamushi (Hatai & Ohfuchi, 1937); MIYAGI-KEN Aji-shima, Ashi-jima, Eno-shima, Hira-jima, Izu-shima, Kinkazan, Kunimitōge near Sendai, Onagawa, O-shima & Tashiro-jima (Hatai & Ohfuchi, 1937).

DISTRIBUTION. Japan.

Metaphire sieboldi (Horst, 1883)

sieboldi Horst, 1883 : 191. Other Japanese records: Rosa, 1891 : 401; Michaelsen, 1892 : 235; Hatai, 1931 : 398; Kobayashi, 1941b : 260, c : 378, e : 513 [non Goto & Hatai, 1898 : 65; Beddard, 1892b : 759 (= *hilgendorfi* species-complex)].
setosa Cognetti, 1908 : 1.

DIAGNOSIS. Spermathecal pores paired, c. 0·31 body circumference apart in furrows 6/7/8/9. Male pores within shallow copulatory pouches on segment 18. Secretory diverticula absent. Genital markings absent. Intestinal caeca manicate, each usually with 5 diverticula, originating in segment 27.

JAPANESE RECORDS. 'Japan' (Horst, 1883; Rosa, 1891; Michaelsen, 1892). **Honshu (Chūbu-Chihō)** (Kobayashi, 1941b & c): **(Kinki-Chihō)** (Kobayashi, 1941b & c): **(Chūgoku-Chihō)** (Kobayashi, 1941b & c). **Shikoku** (Hatai, 1930; Kobayashi. 1941b & c); TOKUSHIMA-KEN (Cognetti, 1908). **Kyushu** (Kobayashi, 1941b, c & e); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941c); KAGOSHIMA-KEN Kagoshima, Kaimon-dake & Kirishima Yama (Kobayashi, 1941c).

DISTRIBUTION. Japan.

Metaphire tosaensis (Ohfuchi, 1938)

tosaensis Ohfuchi, 1938c : 58. Other Japanese records: Kobayashi, 1941b : 260, c : 378.

DIAGNOSIS. Spermathecal pores paired, c. 0·25 body circumference apart in furrows 5/6/7/8/9. Male pores in copulatory pouches restricted to segment 18. Genital markings absent. Intestinal caeca simple with incised dorsal margins, originating in segment 27.

JAPANESE RECORDS· **Honshu (Kinki-Chihō)** NARA-KEN Tosa (Ohfuchi, 1938c). **Shikoku**

(Kobayashi, 1941*b* & *c*). **Kyushu** (Kobayashi, 1941*b* & *c*); MIYAZAKI-KEN Aoi-dake (Kobayashi, 1941*c*); KAGOSHIMA-KEN Kagoshima & Kirishima Yama (Kobayashi, 1941*c*).

DISTRIBUTION. Japan.

Metaphire yamardai (Hatai, 1930)

yamardai Hatai, 1930*b* : 664. Other Japanese records: Kobayashi, 1941*b* : 260.
soulensis Kobayashi, 1938*a* : 131. Other Japanese records: Kobayashi, 1941*a* : 51, *b* : 260, *c* : 378, *e* : 513.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·43 body circumference apart in furrows 6/7/8/9. Male pores within copulatory pouches on segment 18. Genital markings small, median to the spermathecal pores on segments 7 and 8, and within the copulatory pouches. Intestinal caeca manicate each with 5 or 6 diverticula, originating in segment 27.

JAPANESE RECORDS.   **Honshu (Chūbu-Chihō)** (Kobayashi, 1941*b* & *c*); ISHAKAWA-KEN Hatta (Hatai, 1930*b*): **(Kinki-Chihō)** (Kobayashi, 1941*b* & *c*); HYOGO-KEN Kōbe (Hatai, 1930*b*); WAKAYAMA-KEN (Hatai, 1930*b*): **(Chūgoku-Chihō)** (Kobayashi, 1941*b* & *c*); TOTTORI-KEN (Hatai, 1930*b*); SHIMANE-KEN Oki-guntō (Kobayashi, 1941*a* & *b*); OKAYAMA-KEN (Hatai, 1930*b*). **Shikoku** (Kobayashi, 1941*b* & *c*). **Tsushima** (Kobayashi, 1941*b*). **Kyushu** (Kobayashi, 1941*b*, *c* & *e*); KAGOSHIMA-KEN Kaimon-dake (Kobayashi, 1941*c*).

DISTRIBUTION. Japan, China, Korea.

Metaphire yezoensis (Kobayashi, 1938)

yezoensis Kobayashi, 1938*b* : 412.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·29 body circumference apart in furrows 5/6/7/8. Male pores in copulatory pouches on segment 18. Genital markings absent. Intestinal caeca simple with incised ventral margins, originating in segment 27.

JAPANESE RECORDS.   **Hokkaido** OSHIMA Hakodate (Kobayashi, 1938*b*).

DISTRIBUTION. Japan.

Pheretima (Parapheretima) koellikeri Michaelsen, 1928

Pheretima sp. Michaelsen, 1903 : 100.
koellikeri Michaelsen, 1928 : 8. Other Japanese records: Kobayashi, 1941*e* : 513.
??vesiculata Goto & Hatai, 1899 : 21.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·40 body circumference apart in furrows 6/7/8. Spermathecal diverticula present. Male pores in copulatory pouches in the setal line of segment 18. Secretory diverticula discharge into copulatory pouches. Genital markings absent. Intestinal caeca manicate, each with several diverticula, originating in segment 27.

JAPANESE RECORDS. 'Japan' (Michaelsen, 1928). **Honshu (Kantō-Chihō)** IBARAKI-KEN Oarai (Goto & Hatai, 1899): **(Chūgoku-Chihō)** OKAYAMA-KEN Takahashi (Goto & Hatai, 1899). **Kyųshu** (Kobayashi, 1941*e*).

DISTRIBUTION. Japan.

Pithemera bicincta (Perrier, 1875)

bicincta Perrier, 1875 : 1044. Japanese records: Ohfuchi, 1957 : 254.

DIAGNOSIS. Spermathecal pores paired, *c.* 0·26 body circumference apart in furrows 4/5/6/7/8/9. Male pores superficial on segment 18. Genital markings large paired median to male pores and extending onto segments 17 and 19. Intestinal caeca simple with smooth margins, originating in segment 22.

JAPANESE RECORDS. **Sakishima-Guntō** ISHIGAKI-SHIMA Ibarama (Ohfuchi, 1957); IRIOMOTE-JIMA Hatoma-jima (Ohfuchi, 1957).

DISTRIBUTION. Indigenous range uncertain. This species has been introduced into many parts of the world by man (for details see Gates, 1972a : 170).

Polypheretima elongata (Perrier, 1872)

elongata Perrier, 1872 : 124; Easton, 1979 : 53. Japanese records: Kobayashi, 1941c : 378 [non Ohfuchi, 1956 : 148 (= *Amynthas morrisi*)].
biserialis Perrier, 1875 : 1044. Japanese records: Ohfuchi, 1956 : 151.

DIAGNOSIS. Spermathecal pores absent or in paired ventrolateral batteries of 0–5 pores in furrows 5/6 or 6/7 or 5/6/7. Male pores in copulatory pouches on segment 18. Genital markings large, paired, presetal, in line with the male pores on segments 19–24. Intestinal caeca absent.

JAPANESE RECORDS. **Okinawa-Guntō** OKINAWA-JIMA (Kobayashi, 1941c); Higaki (Ohfuchi, 1956). **Sakishima-Guntō** IRIOMOTE-JIMA Obama-jima (Ohfuchi, 1956).

DISTRIBUTION. Indigenous range: East Java, ? Madura, Bali, Lombok, Flores, ? south Celebes (Easton, 1976 : 41). Introduced into many parts of the world by man (Easton, 1979 : 53).

Polypheretima iizukai (Goto & Hatai, 1899)

iizukai Goto & Hatai, 1899 : 14; Easton, 1979 : 43. Other Japanese records: Ohfuchi, 1937b : 39; Kobayashi, 1941b : 260.

DIAGNOSIS. Spermathecal pores paired in furrows 5/6/7/8/9. Male pores superficial on small porophores on segment 18. Genital markings large, paired, postsetal, in line with the male pores on segments 19–23. Intestinal caeca absent.

JAPANESE RECORDS. **Honshu (Kantō-Chihō)** (Kobayashi, 1941b); 'Mt Takao, near Tokyo' (Ohfuchi, 1937b); SAITAMA-KEN (Goto & Hatai, 1899); **(Chūbu-Chihō)** (Kobayashi, 1941b).

DISTRIBUTION. Japan.

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British Museum (Natural History) 1881–1981

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Phylogenetic versus convergent relationship
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Melanie L. J. Stiassny

Phylogenetic versus convergent relationship between piscivorous cichlid fishes from Lakes Malawi and Tanganyika

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Contents

Synopsis

The anatomy and phylogenetic relationships of two genera of African cichlid fishes, *Rhamphochromis* from Lake Malawi and *Bathybates* from Lake Tanganyika, are investigated. In accordance with the current methods of cladistic analysis data from representatives of a wide range of cichlid taxa are included for outgroup comparison. Particular emphasis is placed upon the anatomy of the ethmovomerine region of the neurocranium, the cheek musculature, and the pharyngeal jaw apparatus.

Based upon a number of synapomorphic characters an hypothesis of a sistergroup relationship between the monophyletic genus, *Bathybates*, and a monophyletic assemblage consisting of the genera *Hemibates* and *Trematocara* is formulated. A similar resolution of the relationships of *Rhamphochromis* has not been achieved; the differential success of the study is discussed and additional data relevant to unravelling the status and relationships of *Rhamphochromis* are introduced.

Introduction

The similarities that exist between individual species and whole communities of cichlid fishes in Lakes Malawi and Tanganyika have often been remarked upon (eg. Pellegrin, 1903; Regan, 1921, 1922; Fryer, 1959; Fryer & Iles, 1972; Galis & Barel, 1980). Regan (1921) felt that the majority of the Malawian genera were phyletically distinct from any found elsewhere and that they formed a 'natural group'. Since that time, because it has been assumed that the cichlid flock of each lake has had a separate ancestry, their similarities have been interpreted as examples of convergent evolution (Fryer, 1969; Fryer & Iles, 1972).

The recent papers of Greenwood (1978, 1979, 1980) cast considerable doubt upon existing ideas about the phylogeny and interrelationships of the lacustrine Cichlidae. With reference

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to the Lake Malawi haplochromine species group Greenwood (1979) suggests that the prevalent idea of the Malawi group being entirely derived from one or a few anatomically generalized fluviatile haplochromine cichlids (see Regan, 1921; Trewavas, 1935, 1949; Greenwood, 1974) is an oversimplification. He now suspects that lineages related to *Thoracochromis, Astatotilapia,* and even to *Serranochromis* and *Chetia* may have contributed to the flock. Clearly there is a need to reconsider the phyletic relationships of these lacustrine Cichlidae.

Apart from the large number of species the problem of determining the interrelationships of the lacustrine Cichlidae is intensified by the fact that few characters have been found to be of use in phylogenetic analyses. The common occurrence of a range of morphological features confers a rather characteristic 'facies' upon many trophic groups (Greenwood, 1974). The problem of determining monophyletic assemblages, on the basis of shared derived characters, in the face of an apparent 'web of parallelisms' (Liem, 1978) is therefore particularly acute amongst these lacustrine Cichlidae. The two genera that form the subject of the present investigation, *Bathybates* Boulenger, 1898 from Lake Tanganyika and *Rhamphochromis* Regan, 1921 from Lake Malawi, have been selected for a number of reasons. Superficially, at least, *Bathybates* and *Rhamphochromis* are rather similar in external appearance, and Boulenger (1898) suggested that *Bathybates ferox* and *Paratilapia longiceps* (=*Rhamphochromis longiceps*) were closely related. Later, because Regan (1921) felt that the Malawian flock was a natural group, *Rhamphochromis* and *Bathybates* were considered to be an example of convergent evolution (Fryer & Iles, 1972; Lowe-McConnell, 1975).

Although data on the habits and ecology of these fishes are sparse it would appear that both occupy broadly similar biological positions in their respective lakes (Poll, 1956; Coulter, 1966, 1967; Fryer & Iles, 1972; Lowe-McConnell, 1975). Both are essentially off-shore, open-water predators feeding upon cichlid as well as non-cichlid members of the pelagic communities. Species in both genera are also known to frequent the benthic zone where they are able to adapt to the prevailing near anoxic conditions (Coulter, 1967; Lowe-McConnell, 1975).

The fact that both *Bathybates* and *Rhamphochromis* are exclusively piscivorous has also been a factor contributing to their selection for a comparative study. Amongst the trophic groups represented in the lacustrine flocks the piscivorous predatores comprise one of the largest groups (c.30–40% of total species number). The large number of piscivorous species seems to be attributable both to the large biomass of other cichlid species (Fryer & Iles, 1972; Witte, in press) and to the apparently minor anatomical modification necessary to facilitate the capture and ingestion of this food source (Fryer & Iles, 1972; Liem, 1978).

Methods, nomenclature and materials

Methods

In order to determine the phylogenetic relationships of *Bathybates* and *Rhamphochromis* a cladistic approach has been adopted. Monophyletic groups are defined on the basis of shared derived characters (synapomorphies), and in estimating the relative plesiomorph (primitive) or apomorph (derived) nature of various character states the 'commonality principle' (Schaeffer, Hecht and Eldredge, 1972) is applied.

A number of problems arise when cladistic principles are applied to an analysis of cichlid interrelationships (see Greenwood, 1979: 270). Apart from the phylogenetic breakdowns provided by Greenwood (1979, 1980), Liem and Stewart (1976) and Liem (1979) little guidance is available to aid the selection of appropriate cichlid outgroup taxa. Highly tentative and noncladistic phylogenies for members of the Lake Malawi and Lake Tanganyika flocks are to be found in Fryer & Iles (1972) (see also Regan, 1920, 1921, 1922; Trewavas, 1949). In the course of this investigation those taxa which have been thought by these authors to be 'close to' or 'implicated in the ancestry' of *Bathybates* or *Rhamphochromis*

have received particular attention. I have also placed an emphasis upon the examination of other lacustrine taxa although some riverine forms have been included. Otherwise my selection of cichlid outgroup taxa has been somewhat arbitrary.

The following review is a partial account of the anatomy of selected cichlid taxa. Only those structures found to yield characters suitable for phylogenetic analysis at the level of universality under consideration have been selected for description here. Characteristics of the ethmovomerine region of the neurocranium, the cheek musculature and the pharyngeal jaw apparatus (PJA *sensu* Hoogerhoud & Barel, 1978) receive particular attention.

Descriptions are based upon the type species, *Rhamphochromis longiceps* and *Bathybates ferox*, of the two major genera and where possible also of the type species of outgroup genera.

For more detailed and comprehensive accounts of cichlid anatomy see Goedel (1974a, b) and Anker (1978) for myology, and Barel *et al.* (1976) for osteology.

Nomenclature

The nomenclature of muscles follows that of Winterbottom (1974) and Anker (1978). Topographical and skeletal nomenclature is based upon that of Nelson (1969), Rosen (1973), Patterson (1975) and Barel *et al.* (1976).

To investigate myological structures specimens were dissected under a Wild M-7 stereomicroscope. Osteological study specimens were cleared in buffered trypsin solution and double stained following the procedure of Dingerkus & Uhler (1977). This material was supplemented by reference to the extensive osteological collections in the British Museum (Natural History).

Taxonomic nomenclature

Greenwood (1979) divides the polyphyletic genus *Haplochromis* into a number of monophyletic lineages (=genera) restricting *Haplochromis* to five species. Difficulties arise when reference is made either to species formerly included within the genus but have yet to be assigned to other genera, or to the former concept of the genus *Haplochromis*. To avoid confusion Greenwood (1979) suggests adopting a convention proposed by Patterson & Rosen (1977). Thus the specific names of species formerly placed in the genus *Haplochromis* and not allocated to other genera will be prefixed with the name *Haplochromis* cited between quotation marks. When referred to collectively all cichlid fishes with an *Haplochromis* type of pharyngeal apophysis (Greenwood, 1978) are termed haplochromine cichlids.

Taxonomic note on Bathybates and Rhamphochromis

The genus *Bathybates* is entirely restricted to Lake Tanganyika and was originally described by Boulenger (1898; type species *Bathybates ferox* Boulenger, 1898). Boulenger (1898) believed that *Bathybates* was closely related to *Paratilapia* with which it was connected by *Paratilapia longiceps* Günther (=*Rhamphochromis longiceps*) of Lake Malawi. He believed that the more formidable dentition coupled with characters of the body scales warranted the establishment of a new genus.

Since that time six more *Bathybates* species have been described; *Bathybates fasciatus* Boulenger, 1901; *Bathybates vittatus* Boulenger, 1914; *Bathybates minor* Boulenger, 1906; *Bathybates graueri* Steindachner, 1911; *Bathybates horni* Steindachner, 1911; *Bathybates leo* Poll, 1956. A key to the species of *Bathybates* can be found in Poll (1956).

In 1915 Boulenger brought together *Paratilapia caerulea* Boulenger, 1908, *Paratilapia esox* Boulenger, 1908 and *Hemichromis longiceps* Günther, 1864 into a new genus, *Champsochromis*. Regan (1921) was of the opinion that the type species of that genus, *Champsochromis caeruleus*, was not generically distinct from *Haplochromis* as then defined and therefore placed *caeruleus* in *Haplochromis*. For the remaining species he established the genus *Rhamphochromis*, and designated *Rhamphochromis longiceps* the type species. He added four additional species to his genus: *Rhamphochromis macrophthalmus* Regan, 1921;

Rhamphochromis ferox Regan, 1921; *Rhamphochromis woodi* Regan, 1921, and *Rhampho-chromis leptosoma* Regan, 1921. Since that time two more species have been described: *Rhamphochromis lucius* Ahl, 1926 and *Rhamphochromis brevis* Trewavas, 1935. A key to the species of *Rhamphochromis* can be found in Trewavas (1935). Unlike *Bathybates*, *Rhamphochromis* is not exclusively lacustrine and specimens have been collected in the Upper Shiré River (Boulenger, 1915; Ricardo-Bertram *et al.*, 1946; pers. obs.). More species of *Rhamphochromis* from Lake Malawi, particularly from the Nkata Bay region, have yet to be described (pers. obs.).

Materials

Material representative of the following cichlid genera has been examined. A complete list of specimens used in this study is deposited in the fish section of the British Museum (Natural History). The number in brackets following each generic name indicates the number of species examined.

South American genera:

Acaronia (1)	*Astatotilapia* (5)	*Lichnochromis* (1)
Aequidens (1)	*Aulonocara* (2)	*Limnochromis* (2)
Apistogramma (1)	*Aulonocranus* (1)	*Limnotilapia* (1)
Cichla (1)	*Bathybates* (7)	*Neotilapia* (1)
Cichlasoma (4)	*Boulengerochromis* (1)	*Orthochromis* (1)
Crenicichla (3)	*Callochromis* (1)	*Perissodus* (3)
Geophagus (3)	*Chetia* (1)	*Pharyngochromis* (1)
Petenia (1)	*Ctenochromis* (1)	*Prognathochromis* (3)
	Diplotaxodon (1)	*Rhamphochromis* (8)
Asian genera:	*Ectodus* (1)	*Sarotherodon* (1)
Etroplus (2)	*Haplochromis* (1)	*Serranochromis* (5)
	'Haplochromis' (25)	*Teleogramma* (1)
Madagascan genera:	*Haplotaxodon* (1)	*Telmatochromis* (2)
Paratilapia (1)	*Hemibates* (1)	*Tilapia* (1)
Paretroplus (1)	*Hemichromis* (1)	*Trematocara* (8)
Ptychochromis (1)	*Hemitilapia* (1)	*Trematocranus* (1)
	Lamprologus (10)	*Tylochromis* (2)
African genera:	*Lethrinops* (2)	*Xenotilapia* (2)
Aristochromis (1)		

Abbreviations used in the text figures

A_1, A_2, A_3, A_w	parts of the adductor man-dibulae muscle
aa	anguloarticular
aap	adductor arcus palatini muscle
ad5	5th adductor muscle
ad-fos	adductor fossa
art.fc-pb3	articulatory facet of pharyn-gobranchial 3
asp-aa	ascending process of the anguloarticular
asp-aa.f	flange on ascending process of the anguloarticular
ca	central aponeurosis
cart.ext.ep2	cartilaginous extension of epibranchial 2

cc	cranial condyle
con.tiss.tract	connective tissue tract
cp	coronoid process of the dentary
d-bb	dorsal bony bridge
dent	dentary
dl-f	dorsolateral fenestra
do	dilatator operculi muscle
ect	ectopterygoid
end	endopterygoid
ep1–4	epibranchials 1–4
ex.hd-ep4	expanded head of epibranchial 4
exs	extrascapula
fr	frontal
h-lpe	horn of lower pharyngeal element
hym	hyomandibula
im	intermandibularis muscle
intorb-s	interorbital septum
lac	lachrymal
l.ang-dent	angulodentale ligament
lap	levator arcus palatini muscle
le	lateral ethmoid
le-b	body of lateral ethmoid
le-e	anterior extension of lateral ethmoid
le-p	lateral ethmoid process
lev-ext 1–4	levatores externi muscles 1–4
lev-int 1–2	levatores interni muscles 1–2
lev-post	levator posterior muscle
l-fos	lateral fossa
lo	levator operculi muscle
l.pal-le	palatine-lateral ethmoid ligament
l.pal-mes	palatine-mesethmoid ligament
lpe	lower pharyngeal element
mc	Meckel's cartilage
m.c-p2	musculus cranio-pharyngobranchialis 2
mes	mesethmoid
mes-a	arm of mesethmoid
mes-p	plate of mesethmoid
mes-w	wing of mesethmoid
met	metapterygoid
m.t-e2	musculus transversus epibranchialis 2
m.t-p2	musculus transversus pharyn-gobranchialis 2
mx-f	maxillary flange

nlf 0–5	neurocranial lateral line foramina 0–5
nip-pr	nipple process
od-a	obliquus dorsalis anterior muscle
od-p	obliquus dorsalis posterior muscle
oes	oesophagus
op	operculum
ov-f	ovoid fenestra
pal	palatine
pal-fc	palatine facet
pb 1–3	pharyngobranchials 1–3
pmx-art	articular process of the premaxilla
pmx-asp	ascending process of the premaxilla
pop	preoperculum
postorb	postorbital process
preorb	preorbital process
psh	parasphenoid
pt	posttemporal
quad	quadrate
r-d	retractor dorsalis muscle
r-f	rostral fenestra
rost-cart	rostral cartilage
sc	supracleithrum
shank-s	shank spine
spin.oes	sphincter oesophagi
sym	symplectic
tA_{1a-c}	tendons of A_1
tA_2	tendon of A_2
tA_3	tendon of A_3
tA_w	tendon of A_w
td-p	transversus dorsalis posterior muscle
t.lev-ext3	tendon of levator externus 3 muscle
t.lev-int 1	tendon of levator internus 1 muscle
up-4	fourth upper tooth-plate
V	ramus mandibularis V
vl-f	ventrolateral fenestra
vl-bb	ventrolateral bony bridge
vo-fc	vomerine facet
vo-fos	vomerine fossa
vo-h	head of the vomer
v-s	stalk of the vomer
vo-wing	wing of the vomer

Note on the figures
The scale on all figures indicates 5 mm

Anatomical description

The ethmovomerine region of the neurocranium

Because of the position of the ethmovomer it acts as a base upon which the premaxillae move and are supported (Alexander, 1967; Rosen & Patterson, 1969). It is thus of importance in feeding and hence trophic adaptation, one of the key elements in the ecological success of lacustrine Cichlidae (Fryer & Iles, 1972; Greenwood, 1974).

As in most higher teleosts, the ethmovomer of the Cichlidae is composed of four bones: the paired lateral ethmoids, the mesethmoid and the vomer. Both the mesethmoid and the vomer are compound elements incorporating a number of dermal components (Patterson, 1975). The modal arrangement of these bones and associated cartilage in the African Cichlidae is illustrated in Fig. 1.
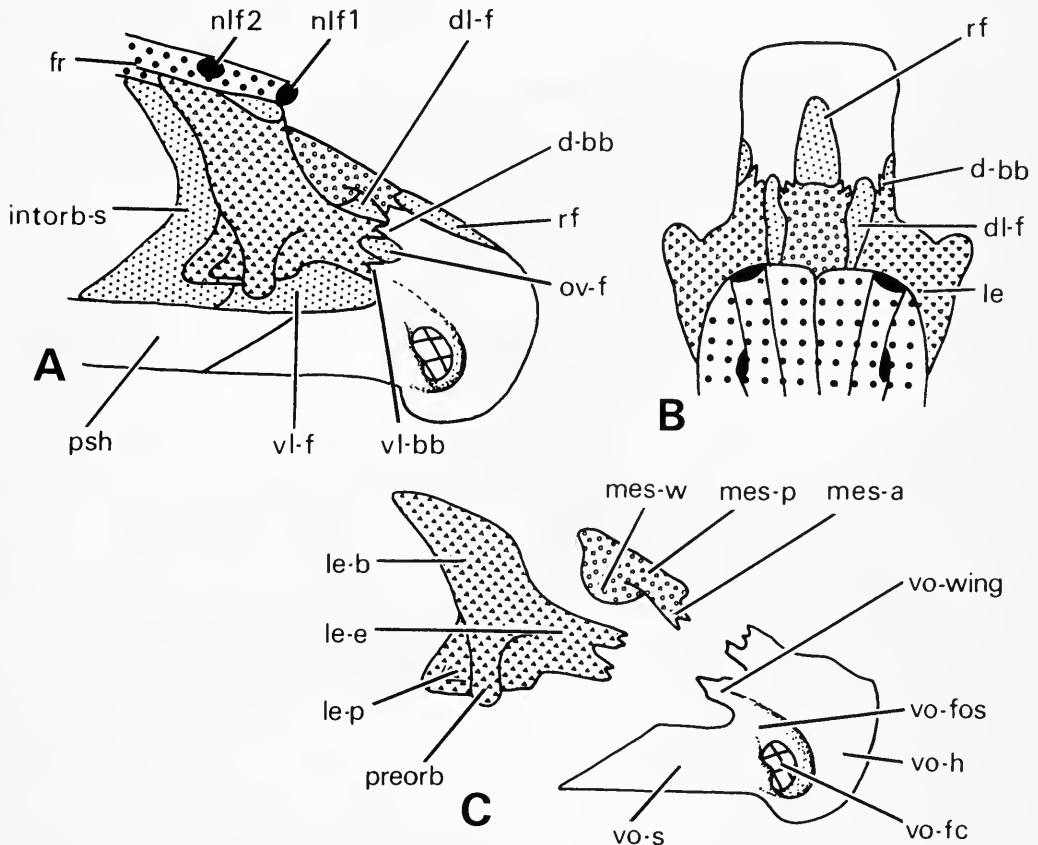
Fig. 1 Semidiagrammatic drawing of the modal arrangement of the bones of the ethmovomer in African cichlids. A. Lateral view. B. Dorsal view. C. Lateral view (exploded).

Regan (1920) was the first to attribute any phylogenetic significance to the particular associations of the bones in this region of the skull in cichlid fishes. He divided the genus *Tilapia* into a number of subgenera using the presence or absence of a sutural connection between the mesethmoid (=ethmoid of Regan, 1920) and the vomer as one of the characters for so doing. Trewavas (1973), Liem & Stewart (1976) and Liem (1979) also utilize ethmovomer characteristics in phylogenetic analyses of cichlid fishes. None of these authors has discussed the relationship of the lateral ethmoid bones to the other bones of that region.

Rhamphochromis

The lateral ethmoid bones (Figs 2 & 13A)

The elongate lateral ethmoids form the posterolateral part of the ethmovomer. The two bones are separated posteromedially by a cartilaginous interorbital septum and anteromedially by the mesethmoid and the ethmovomerine cartilage. Each bone may be described in two parts; the body and the anterior extension.

Dorsally the body contacts the frontal and ventrally it forms the floor, anterior wall and side of the anterior myodrome. Medially it bears a large well developed process (the lateral ethmoid process) which abuts against the ethmovomerine cartilage.

The anterior extension of the lateral ethmoid is suturally united with the vomer at two separate points. The dorsal sutural contact (the dorsal bony bridge) is separated from the lateroventral contact (the lateroventral bony bridge) so that the ethmovomerine cartilage is bridged dorsally and ventrally to expose an ovoid region of cartilage (the mesethmoid palatinad articulation facet of Barel *et al.*, 1976).

A broad strap-like ligament, the palatine-lateral ethmoid ligament, originates from the ventral face of the anterior extension of the lateral ethmoid and attaches to the laterodorsal ridge on the palatine.
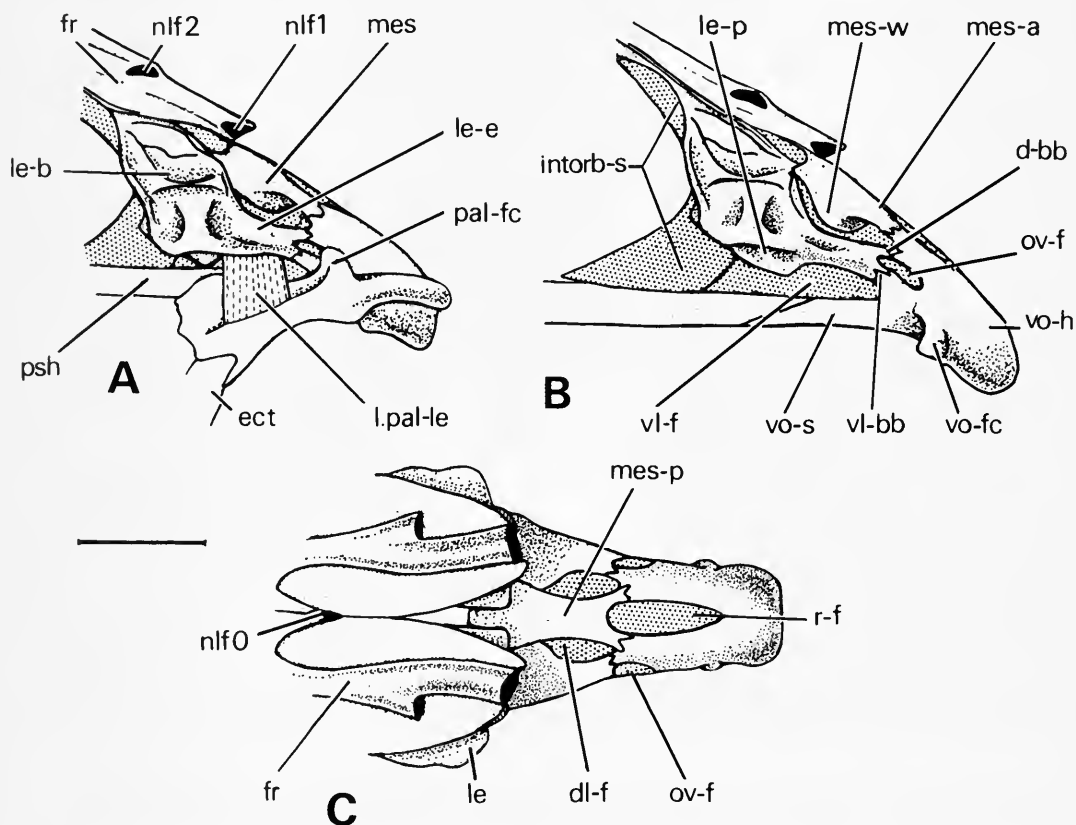
Fig. 2 *Rhamphochromis longiceps,* ethmovomerine region. A. Lateral view. B. Lateral view (suspensorium removed). C. Dorsal view.

The mesethmoid (Figs 2 & 13A)

The mesethmoid is a single, elongate bone situated medially and forming the posterodorsal part of the ethmovomer. The dorsal plate of the mesethmoid underlies the frontal bones forming the floor of the large frontal fossa. Anteriorly the dorsal plate is bifurcated and each

arm of bone is suturally united with the vomer medial to its dorsal suture with the lateral ethmoid. Between the two arms of the mesethmoid the ethmovomerine cartilage is exposed; the anterior margin of the mesethmoid forms the posterior margin of the rostral fenestra. A pair of medial wings are borne on the ventrolateral face of the dorsal plate of the mesethmoid. In lateral view the mesethmoid wings are hemispherical and are separated medially by the ethmovomerine cartilage.

The vomer (Figs 2 & 13A)

The vomer is a large strongly ossified element that forms the anterodorsal and ventral parts of the ethmovomer. It is most conveniently described in two parts: the head and ventral stalk.

The stalk of the vomer is slender and its posterior extremity is enclosed within a channel in the parasphenoid. Dorsally a wing of the stalk is produced above the lateral fossa and becomes suturally united with the lateral ethmoid (the lateroventral bony bridge).

Above the lateroventral bony bridge the head of the vomer is suturally united with the dorsal part of the lateral ethmoid anterior extension (the dorsal bony bridge) and medial to this it is suturally united with the mesethmoid. Dorsomedially the head of the vomer is divided by the rostral fenestra.

The vomer bears a pair of well developed facets for articulation with the palatine.
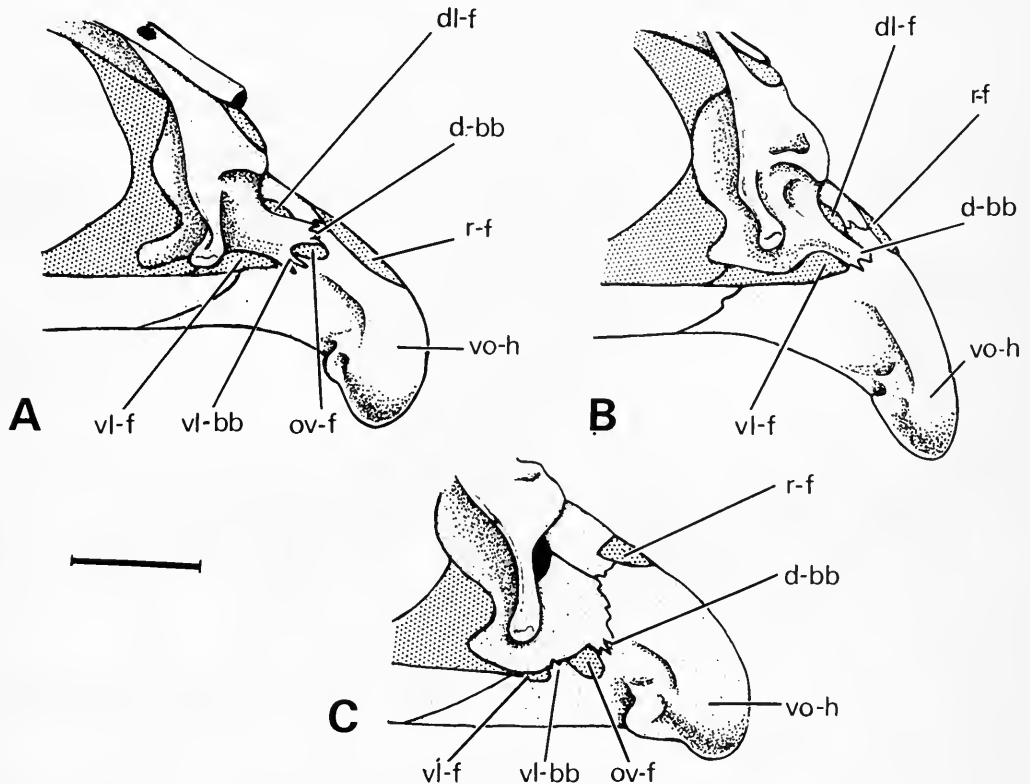

Fig. 3 Ethmovomer (lateral view). A. *Tylochromis lateralis*. B. *Geophagus brasiliensis*. C. *Petenia splendida*.

Bathybates and other cichlid taxa

Outgroup comparisons amongst other cichlid taxa indicate that the arrangement of the bones of the ethmovomer of *Rhamphochromis* represents the modal (ie. plesiomorphic) type found in the majority of African Cichlidae.

Interestingly, in the majority of South American taxa examined the anterior extension of the lateral ethmoid only contacts the vomer dorsally; the ventrolateral bony bridge is absent (compare Fig. 3B of the South American *Geophagus* and Fig. 3A of the African *Tylochromis*). However, in the South American *Petenia* (Fig. 3C) a ventrolateral bony bridge is present, but unlike the 'African' arrangement, in *Petenia* it is the vomer, rather than the vomer and the lateral ethmoid, that is produced to form the bridge.

The ethmovomerine region of *Bathybates* differs from that of *Rhamphochromis* in two salient features:
  (i) the absence of a palatine-lateral ethmoid ligament (Figs 4A & 13B),
  (ii) the reduction or loss of a dorsal bony bridge (Figs 4 & 13B).

The palatine-lateral ethmoid ligament is present in all the other cichlid taxa examined with the notable exceptions of *Hemibates* and *Trematocara* (Figs 5 & 14). Because of the widespread intrafamilial occurrence of this ligament its absence is interpreted as a synapomorphy uniting *Bathybates*, *Hemibates* and *Trematocara*.

A well developed dorsal bony bridge, formed by the sutural union of the anterior extension of the lateral ethmoid and the head of the vomer, is also present in all other taxa except *Bathybates*, *Hemibates* and *Trematocara*. In a few specimens of *Bathybates* and *Hemibates* a narrow splinter of bone has been found linking the lateral ethmoid and the vomer, but in no instance was a well developed dorsal sutural union found. The reduction or loss of the dorsal bony bridge is interpreted as a further synapomorphy uniting the genera *Bathybates*, *Hemibates* and *Trematocara*.

Hemibates and *Trematocara* share a further synapomorphy of the ethmovomerine region; the presence of a palatine-mesethmoid ligament (Fig. 5).

In all of the cichlids examined, the dorsal articulatory facet of the palatine (the mesethmoidad process of Barel *et al.*, 1976) abuts against the lateral aspect of the ethmovomer.
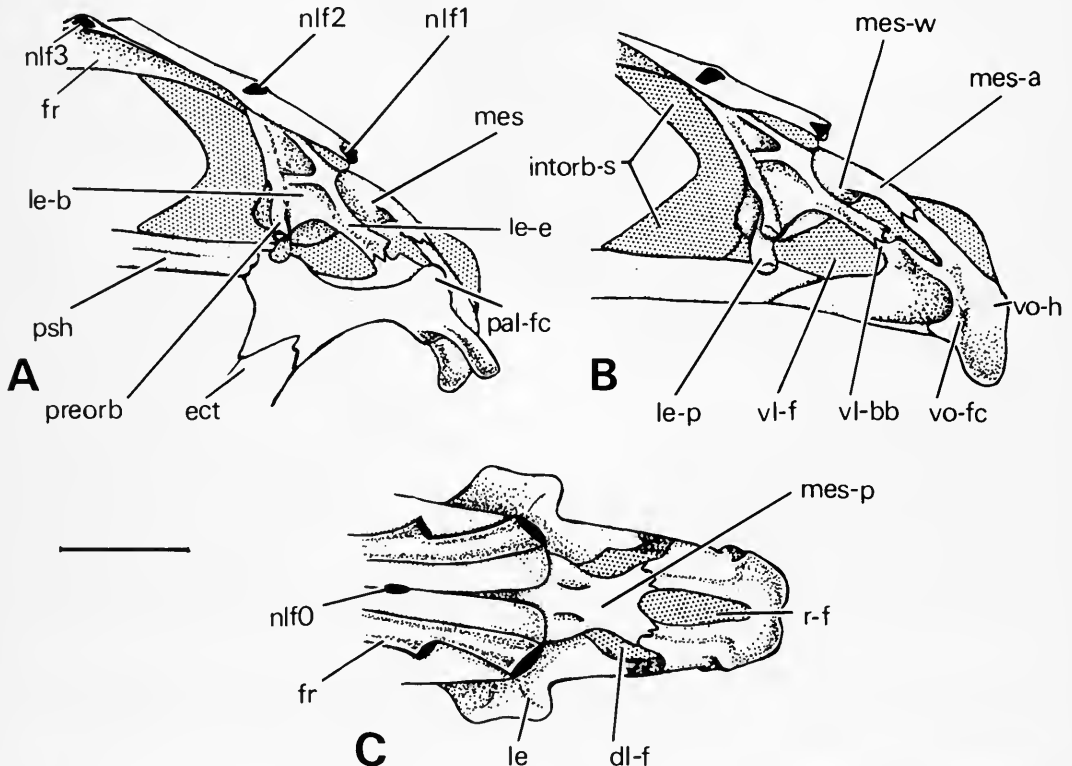
Fig. 4 *Bathybates ferox*, ethmovomerine region. A. Lateral view. B. Lateral view (suspensorium removed). C. Dorsal view.

Whilst in other taxa the facet of the palatine is attached to the ethmovomer by a few strands of connective tissue, in *Hemibates* and *Trematocara* the facet is also attached to the mesethmoid by a palatine-mesethmoid ligament. This ligament arises from the dorsal aspect of the palatine facet and passes posterodorsally to the dorsal face of the mesethmoid. Since it has only been found in *Hemibates* and *Trematocara* it is interpreted as a synapomorphy indicative of a sistergroup relationship between the two genera.

Further evidence of a sistergroup relationship between these two genera is found in the form of the rostral cartilage. In the majority of cichlids each premaxilla has ascending and articular processes and the two ascending processes are closely apposed and firmly bound by connective tissue. The rostral cartilage is a small nubble of cartilage situated on the posterodorsal face of the ascending processes, just above the articular processes. In *Trematocara* and *Hemibates* (Fig. 6C, D), although well developed articular and ascending processes are present, the rostral cartilage is not restricted by them and extends about halfway along the long ascending process. A similar elongation of the rostral cartilage has not been found in any other cichlid taxa.

The premaxillae of *Bathybates* is exceptional since there are no distinct articular processes (Fig. 6B).

The Cephalic muscles

On the basis of their shared innervation the muscles of the cheek may be divided into two groups. The first (group one muscles) includes the adductor mandibulae, the levator arcus palatini, and the dilatator operculi muscles. All are innervated by branches of the fifth
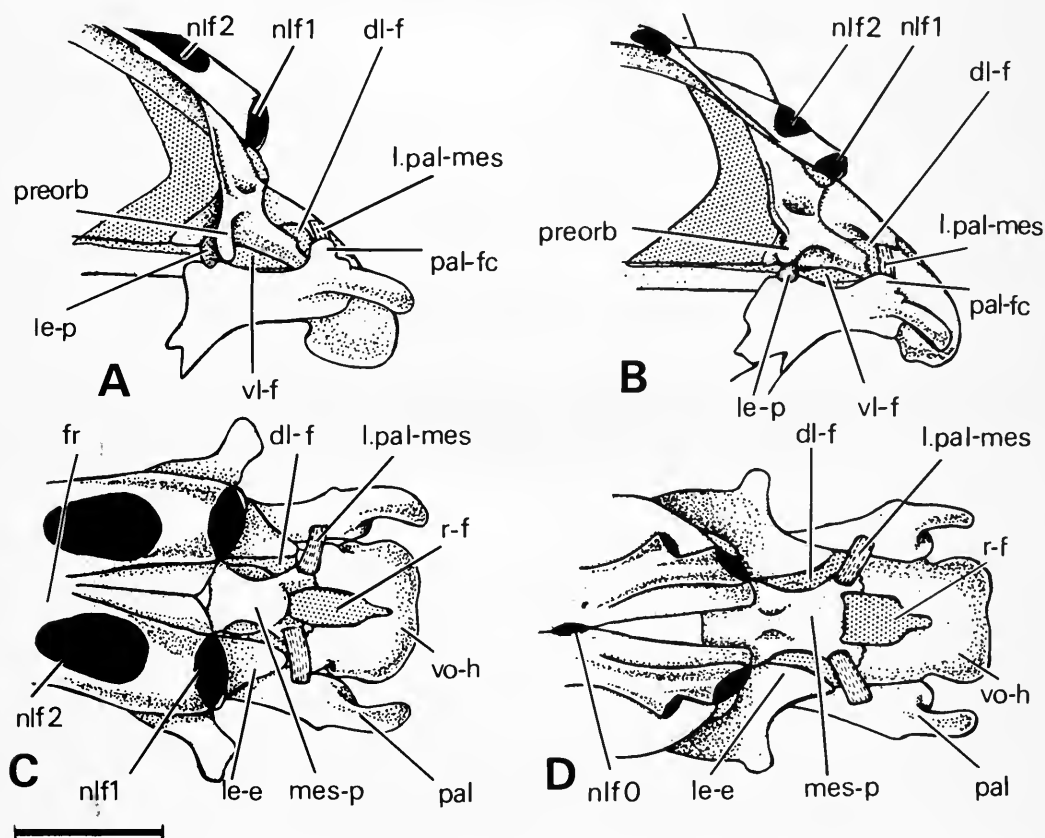
Fig. 5 Ethmovomerine region. Left, *Trematocara marginatum* A. Lateral view. C. Dorsal view. Right, *Hemibates stenosoma* B. Lateral view. D. Dorsal view.

cranial nerve. Group two muscles include the adductor arcus palatini, the adductor operculi and the levator operculi muscles; this group is innervated by branches of the seventh cranial nerve.
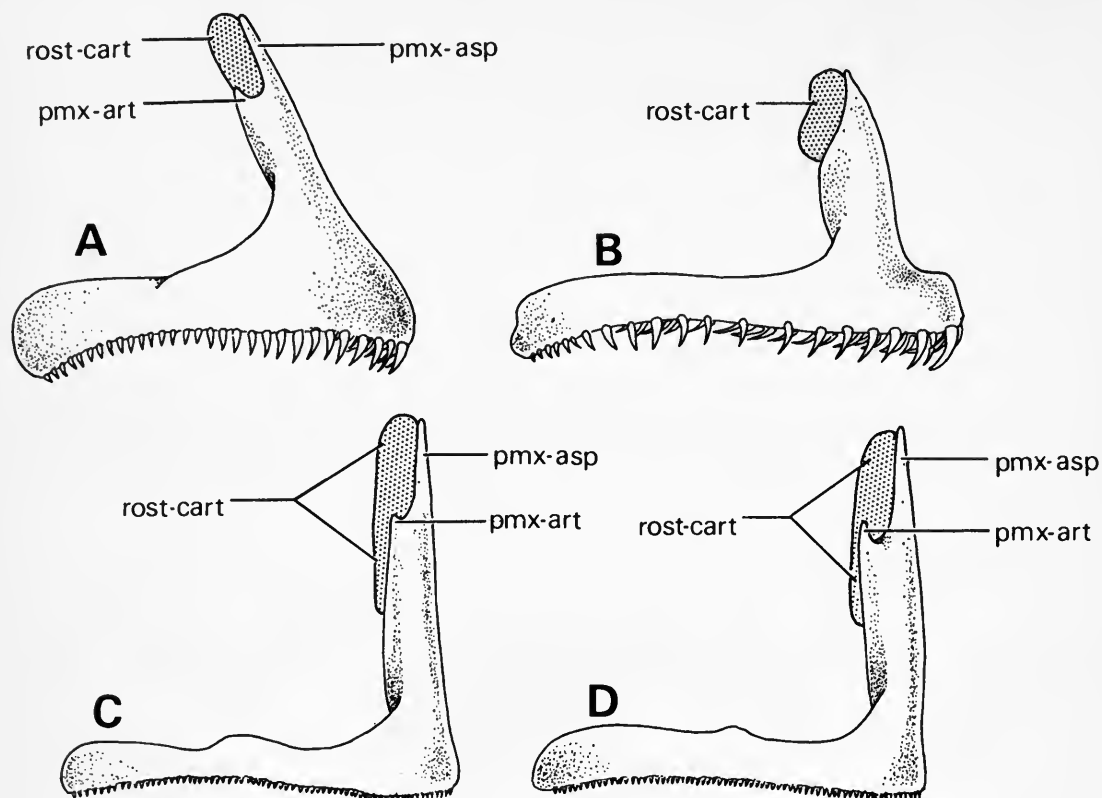
Fig. 6 Right premaxilla (lateral view). A. *Rhamphochromis longiceps.* B. *Bathybates ferox.* C. *Trematocara marginatum.* D. *Hemibates stenosoma.*

Group one muscles

These develop from the masticatory muscle plate which divides early in ontogeny into a dorsal and ventral section. The former gives rise to the constrictor dorsalis and the latter develops into the adductor mandibulae (Edgeworth, 1935).

The adductor mandibulae muscles. This is the largest muscle complex of the head; it occupies the lateral face of the suspensorium and inserts onto both upper and lower buccal jaws. In the Cichlidae four subdivisions are recognized. Following Anker (1978) a distinction is made between a part and a section of a muscle. A part is a subdivision having no, or hardly any, anatomical connection with other subdivisions of the same muscle. A section remains anatomically continuous with the rest of the muscle but may be distinguished from it on the basis of some other criterion such as fibre direction.

Hardly any connection exists between the four subdivisions of the adductor in cichlid fishes. Each part is well defined and easily separable from the others, and each is inserted via a separate tendon.

Although, as compared with some other families, the range of morphological variation of the adductor within the Cichlidae is narrow, numerous small differences are detectable.
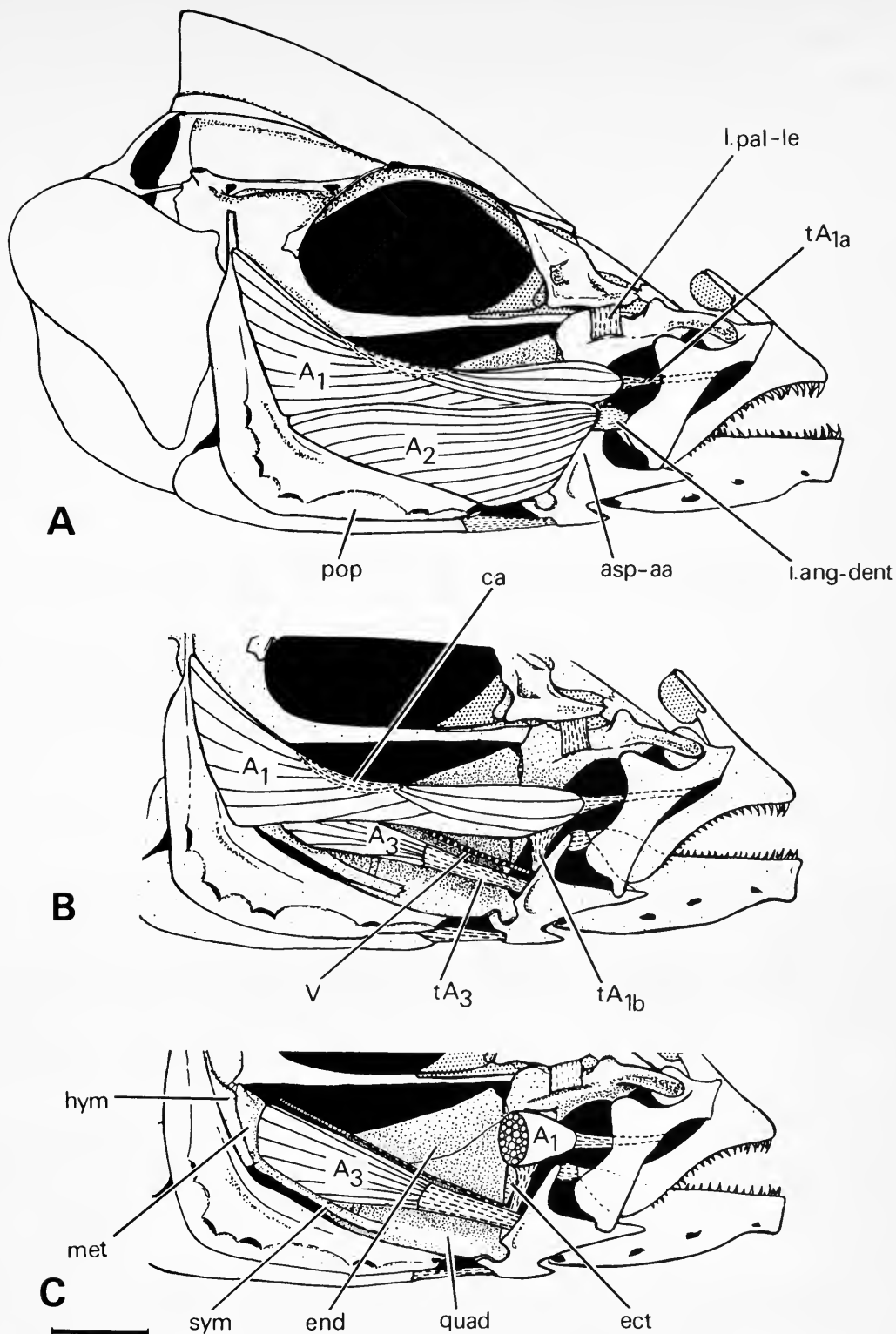
Fig. 7 *Rhamphochromis longiceps.* A. Lateral view of the adductor mandibulae muscle complex after removal of the lachrymal and circumorbital bones and the eyeball. B. After removal of A_2 to expose A_3. C. After the removal of A_2, and with A_1 cut away.

Rhamphochromis

INNERVATION. The path of the ramus mandibularis V is constant. It passes internal to A_1, external and dorsal to A_3, and divides, medial to A_2, sending a minor branch to the anteromedial surface of A_2. The main trunk enters the lower jaw dorsal to the tendon of A_3. On the medial face of the lower jaw the nerve branches, innervating A_w. For a precise description of the course of the ramus mandibularis see Goedel (1974*a, b*) and Anker (1978).

PART A_1 (Figs 7 & 8). This is the dorsal, superficial part of the adductor defined by its dorsal position and insertion onto the maxilla (Vetter, 1874). Part A_1 is a complex elongate muscle which connects the suspensorium with the maxilla and mandible. Origin is from the dorsal face of the vertical limb of the preoperculum and from the hyomandibular transverse zone. Dorsal muscle fibres pass anteroventrally and converge upon a well developed sheet-like aponeurosis situated beneath the eye. The fibres which originate from the middle section of the vertical limb of the preoperculum pass forward, bypassing the dorsal aponeurotic sheet, and intercalate with fibres that have originated from the anterior region of the aponeurosis. Together these fibres converge upon an anteroventral aponeurosis from which two tendons arise. The dorsal tendon, tA_{1a}, passes forward, medial to the maxillary shaft, and inserts on the anterior border of that bone just below the cranial condyle of the maxillary head. The second tendon, tA_{1b}, passes ventrally, medial to tA_3 and the ramus mandibularis V. On the inner aspect of the lower jaw a portion of tA_{1b} intergrades with tA_w, the remainder passes lateral to A_w and inserts onto the nipple process on the anteromedial face of the anguloarticular.

PART A_2 (Fig. 7A). This is the largest component of the adductor. Part A_2 is a parallel-fibred muscle occupying the ventrolateral region of the cheek, connecting the ventral elements of the suspensorium with the lower jaw.

Dorsally A_2 overlies A_1 and it conceals the anteroventral aponeurosis of the latter. Origin is from the crescentic zone and horizontal limb of the preoperculum, the symplectic, and the ventrolateral ridge of the quadrate. Part A_2 is composed of two sections distinguished by their differing sites of insertion. The dorsal section ($A_{2\alpha}$) is composed of fibres originating from the crescentic zone of the preoperculum and inserting onto the coronoid process of the dentary. The fibres contact the coronoid process on its lateral face via an association with the angulodentale ligament and, on its medial face, via a strap-like tendon, tA_2. In the ventral section ($A_{2\beta}$) the fibres originating from the horizontal limb of the preoperculum, the
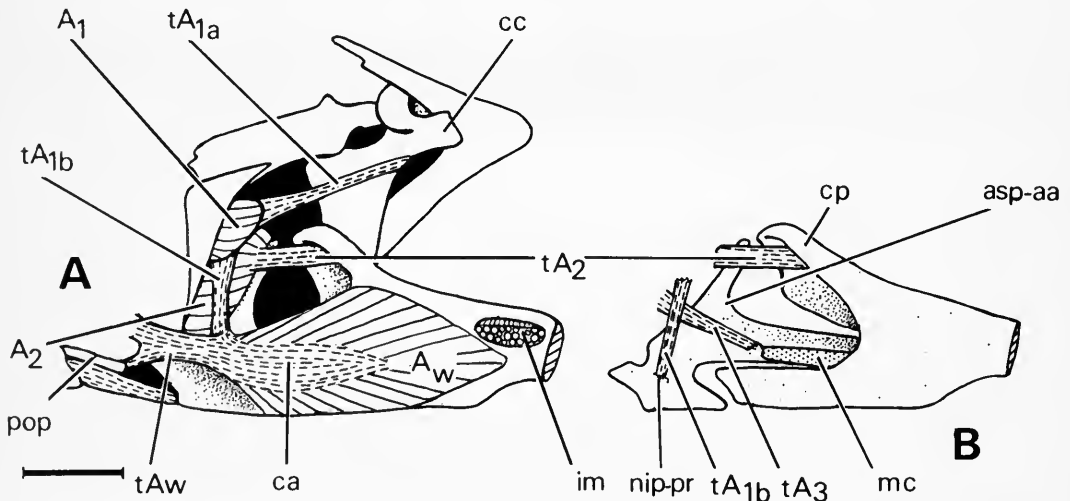

Fig. 8 *Rhamphochromis longiceps*. A. Buccal jaws and anterior suspensorial elements (medial view). B. Dentary, A_2 and A_w removed (medial view).

symplectic, and the quadrate insert musculously onto the posterior border of the ascending process of the anguloarticular. Part A_2 has no connection with part A_w.

PART A_3 (Fig. 7C). This is the medial part of the adductor complex and it underlies both A_1 and A_2. Part A_3 is a small, flat muscle which is roughly triangular in outline with the apex directed rostroventrally. Origin is from the lateral face of the metapterygoid and the dorsal border of the symplectic. Fibres converge upon a well developed strap-like tendon, tA_3 which runs anteroventrally and enters the lower jaw lateral to tA_{1b}. On the inner aspect of the lower jaw tA_3 passes lateral to A_w and inserts onto a small sesamoid ossification (the coronomeckelian ridge of Barel *et al.*, 1976).

PART A_w (Fig. 8A). Part A_w lies on the medial face of the mandible and connects it with the medial face of the suspensorium.

Fibres fan out from a central sheet-like aponeurosis, and attach musculously to the medial face of the coronoid process, the inner and outer walls of the Meckelian fossa and the ventral face of the anguloarticular. Towards the quadrato-mandibular articulation the aponeurosis becomes consolidated into a tendon, tA_w, which is firmly inserted onto the medial face of the quadrate and preoperculum.

THE INTERMANDIBULARIS (Fig. 8A). According to Edgeworth (1935) the mandibular muscle plate, in the early stages of its development, extends from the Gasserian ganglion to the anterior edge of the pericardium or to the midventral line. With the development of Meckel's cartilage the mandibular muscle plate separates into a masticatory muscle plate and the intermandibularis. The latter is innervated by either the ramus mandibularis V (Kesteven, 1943) or it may also receive innervation from the VII cranial nerve.

In the Cichlidae a single intermandibularis is present just caudal to the symphyseal facets of the dentaries. The intermandibularis passes transversely between left and right rami, attaching musculously to their medial faces.

Bathybates

The adductor in *Bathybates* is essentially similar to that of *Rhamphochromis* and a separate description is not warranted. However, certain differences in detail do exist and these are described and illustrated:

(i) The tA_{1a} is considerably reduced in length. The anterior muscle fibres of A_1 have apparently encroached upon the tendon so that the anterior portion of A_1 comes to lie medial to the maxillary shaft (Fig. 9A).

(ii) The short tA_{1a} inserts onto a distinct flange developed on the anterior border of the maxilla, just below the cranial condyle of the maxillary head (Fig. 9A, B).
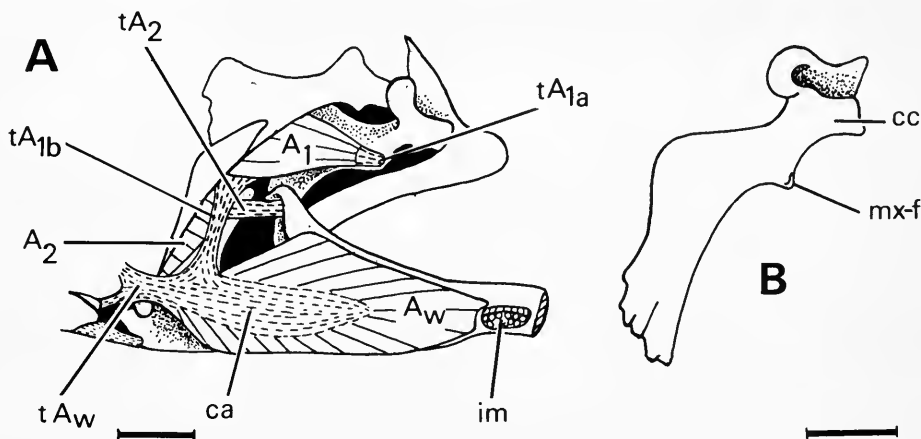

Fig. 9 *Bathybates ferox*. A. Buccal jaws and anterior suspensorial elements (medial view). B. Left maxilla (medial view).

(iii) The posterior face of the ascending process of the anguloarticular is expanded laterally to accommodate a large insertion of section $A_{2\beta}$ (Fig. 10A).

(iv) Part A_3 is large and well developed.

Other cichlid taxa

In the majority of cichlid taxa examined the mode of A_1 insertion is as described in *Rhamphochromis*. The presence of an elongate tA_{1a} is therefore interpreted as a plesiomorphic character of cichlid fishes. The reduction of the length of tA_{1a} in *Bathybates* is, on the basis of its limited distribution, interpreted as a derived character.

Liem (1978: Fig. 6) illustrates the medial aspect of the mandible, maxilla, and the anterior portion of the suspensorium and associated muscles, tendons, and ligaments of *Hemibates stenosoma*. He represents tA_{1a} (tam_1) as a short tendon of the *Bathybates*-type. This contradicts my own observations of tA_{1a} in a range of *H. stenosoma* specimens in which I found tA_{1a} to be of the standard *Rhamphochromis* (i.e. modal) type.

One species of *Lamprologus* (a large genus, most of whose species are endemic to Lake Tanganyika, see Poll, 1978) has a tA_{1a} approaching the *Bathybates* type. This species, *Lamprologus elongatus*, is united with the other *Lamprologus*, none of which has a short tA_{1a}, by the possession of a suite of characters that on the basis of their restricted distribution, are assessed to be apomorphic. For example all *Lamprologus* possess a hyomandibula in which the head is deeply notched, widely spaced extrascapular bones, a prominent flange on the prootic, and the infraorbital bones reduced or absent. All these characters are restricted to *Lamprologus*, or, in the case of infraorbital reduction, also occur in *Telmatochromis, Julidochromis, Chalinochromis,* and *Teleogramma*. In view of the number of synapomorphies uniting *L. elongatus* with the remaining *Lamprologus* species, the presence of a reduced tA_{1a} in *L. elongatus* is interpreted as a convergent development rather than a synapomorphy shared with *Bathybates*.

In all species of *Bathybates* the maxilla bears a distinct flange on its anterior border just below the cranial condyle of the maxillary head. This maxillary flange forms a platform onto which tA_{1a} is firmly inserted. An incipient flange is sometimes present in individual specimens of *Trematocara* and *Hemibates*. The presence of a well developed maxillary flange is interpreted as an apomorphic character within the Cichlidae.
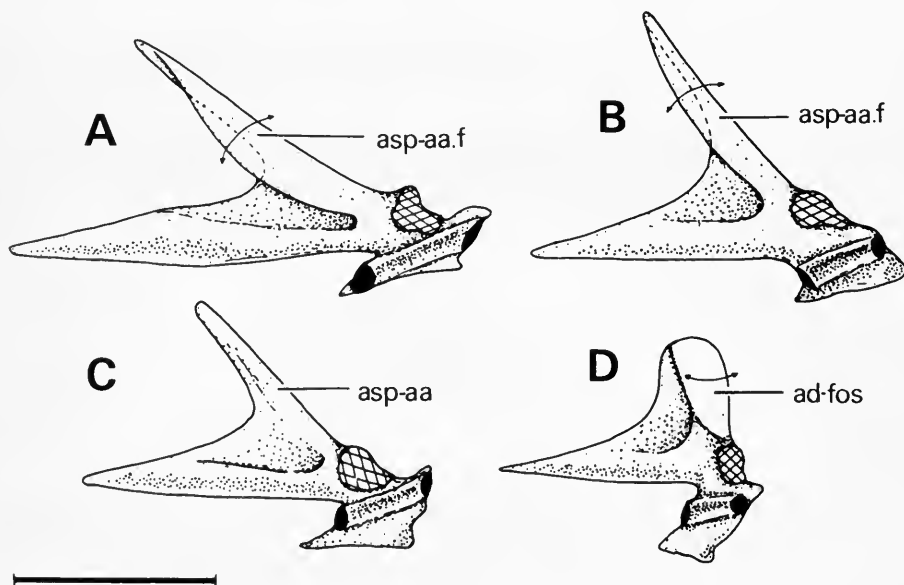

Fig. 10 Left anguloarticular bone. A. *Bathybates ferox*. B. *Trematocara marginatum*. C. *Rhamphochromis longiceps*. D. *Callochromis melanostigma*.

In all species of *Bathybates* (Fig. 10A), *Trematocara* (Fig. 10B), and *Hemibates* the ascending process of the anguloarticular has the posterior border laterally expanded into a ledge on which $A_{2\beta}$ inserts. The presence of this expansion of the anguloarticular is interpreted as a synapomorphy uniting these three genera.

Liem and Osse (1975) describe an adductor fossa in a number of Lake Tanganyika genera. This fossa is an indentation on the lateral face of the anguloarticular (Fig. 10D) which also serves to increase the insertion area of $A_{2\beta}$, and it is of a form quite distinct from that of *Bathybates, Trematocara* and *Hemibates*; it therefore is assessed as an independent character state.

The relatively large A_3 of *Bathybates* is difficult to interpret phylogenetically as there is considerable variation in A_3 development throughout the family.

The A_1 of all *Trematocara* species displays a novel tendinous connection with the lachrymal bone (Fig. 11). In *Trematocara* a third tendon (tA_{1c}) arises from the anteroventral aponeurosis of A_1 and passes forward to insert on the medial face of the large lachrymal bone. A similar connection between the lachrymal and A_1 was not found in any other cichlid taxon examined, and its presence in *Trematocara* is interpreted as a synapomorphy uniting the species of that genus.
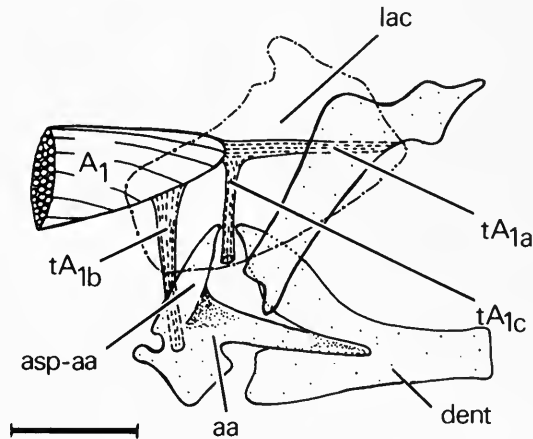
Fig. 11 *Trematocara marginatum*, buccal jaws, lachrymal bone and anterior portion of A_1 (lateral view). The outline of the lachrymal bone is indicated with a broken line.

The dilatator operculi.

Rhamphochromis (Fig. 12A)

The muscle lies behind and above the levator arcus palatini but there is no intercalation of their fibres and the two muscles are distinct. The main muscle mass of the dilatator occupies the well developed dilatator fossa, which is formed anteriorly by the sphenotic and posteriorly by the pterotic bones. The fossa lies between the crest bearing neurocranial lateral line foramina 4, 5 and 6 (Barel *et al.*, 1976) and the hyomandibular articulation sockets. Anteriorly the dilatator is bounded by the postorbital process of the sphenotic bone.

The dilatator origin is extensive, occupying the entire surface of the fossa. Fibres converge ventrocaudally and merge into a tendon-like aponeurosis inserting firmly on the dorsal surface of the dilatator process of the operculum (the dorsal process of Winterbottom, 1974).

Bathybates (Fig. 12B)

The dilatator of *Bathybates* differs from that of *Rhamphochromis* in being expanded anteriorly so that it covers the border of the postorbital process of the sphenotic.

Other cichlid taxa

In all the other cichlid taxa examined, the dilatator operculi is as described for *Rhampho-*

chromis. The anterior expansion of the dilatator in *Bathybates* species is interpreted as a synapomorphy uniting the species of that genus.

The levator arcus palatini. The position and structure of the levator arcus palatini is constant in the taxa examined in this study, although variations were observed in its size and shape. The following brief description of the levator in *Rhamphochromis* is representative of the modal cichlid arrangement.
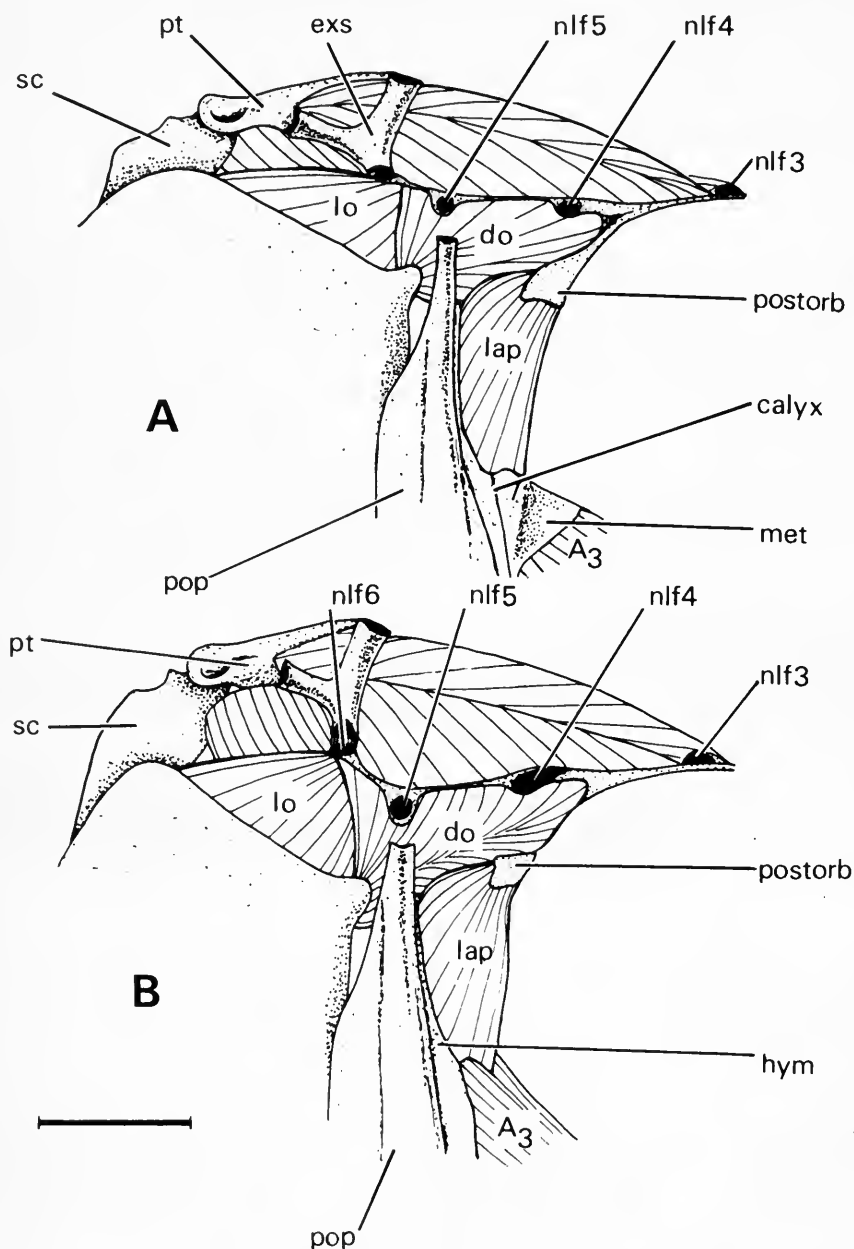
Fig. 12 Superficial postorbital musculature (lateral view) of A. *Rhamphochromis longiceps*. B. *Bathybates ferox*.

Rhamphochromis (Fig. 12A)

The levator is approximately conical in shape with its apex situated dorsally. Origin is from the ventral face of the postorbital process of the sphenotic. The fibres fan out from here and pass ventrally to insert musculously onto the hyomandibular transverse zone and flange, and into the calyx (Barel *et al.*, 1976).

No trenchant differences in the form of the levator in *Bathybates* were recognized.

Group two muscles

All group two muscles are derived from the constrictor hyoideus dorsalis and are innervated by the ramus hyomandibularis of the VIIth cranial nerve (Edgeworth, 1935).

The adductor arcus palatini. The adductor is well developed in the Cichlidae; it extends anteriorly to fill the fissura infraorbitalis and forms the floor of the orbit between the neurocranium and the suspensorium.
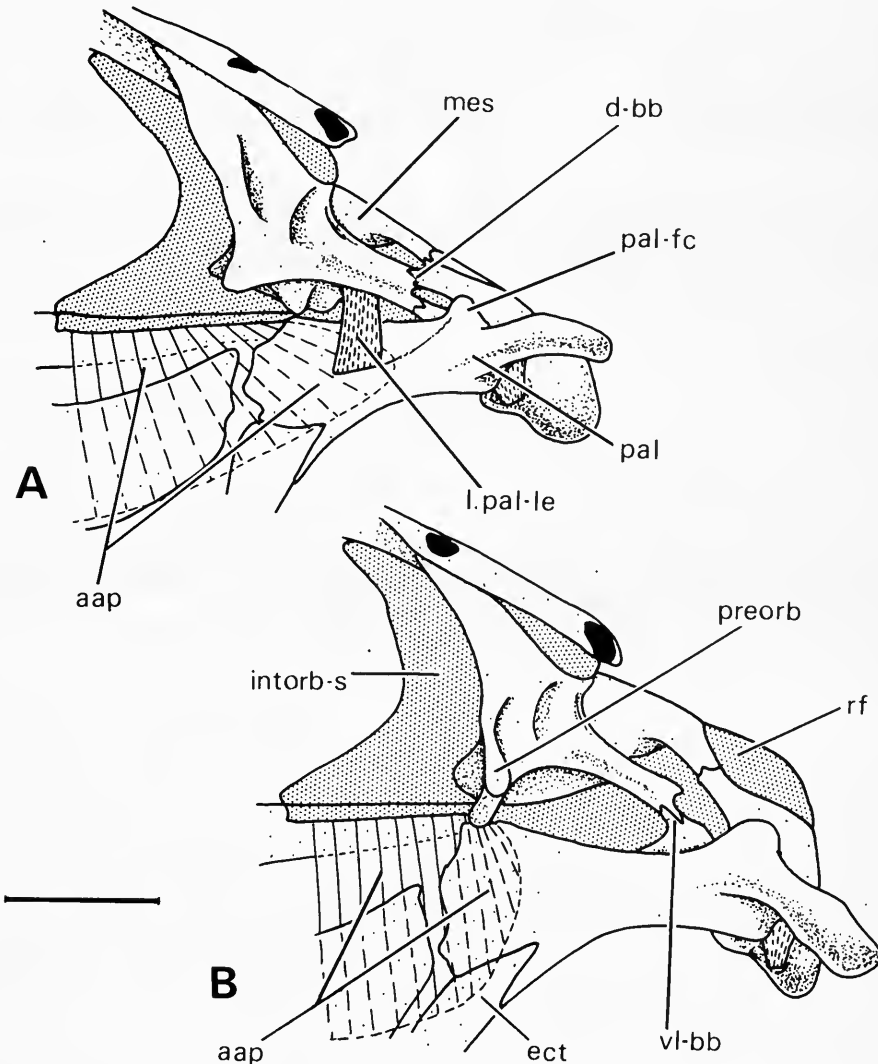
Fig. 13 Ethmovomerine region of A. *Rhamphochromis longiceps.* B. *Bathybates ferox.* The insertion area of the adductor arcus palatini muscle is indicated by broken lines.

Rhamphochromis (Fig. 13A)

The adductor originates musculously from the parasphenoid ventral crest and wing, and from the prootic anteroventral to the lateral commissure. The posterior border of the adductor is demarcated by the prootic-parasphenoid crest.

Fibres originate from the length of the dorsoventral crest of the parasphenoid, and the rostral margin of the muscle lies below the transverse level of the preorbital process. The fibres insert musculously on the medial face of the suspensorium. A sheet of connective tissue originates from the ventromedial face of the lateral ethmoid bones and fans out ventrally to cover the dorsal surface of the adductor.

The posterior fibres pass caudoventrally and insert musculously on the medial face of the hyomandibular flange and the dorsomedial face of the metapterygoid. Anteriorly the muscle fibres slope sharply forward and insert on the medial face of the palatine fossa and the ectopterygoid. The adductor is considerably thicker posteriorly although a slight thickening of the section inserting onto the palatine is discernible.
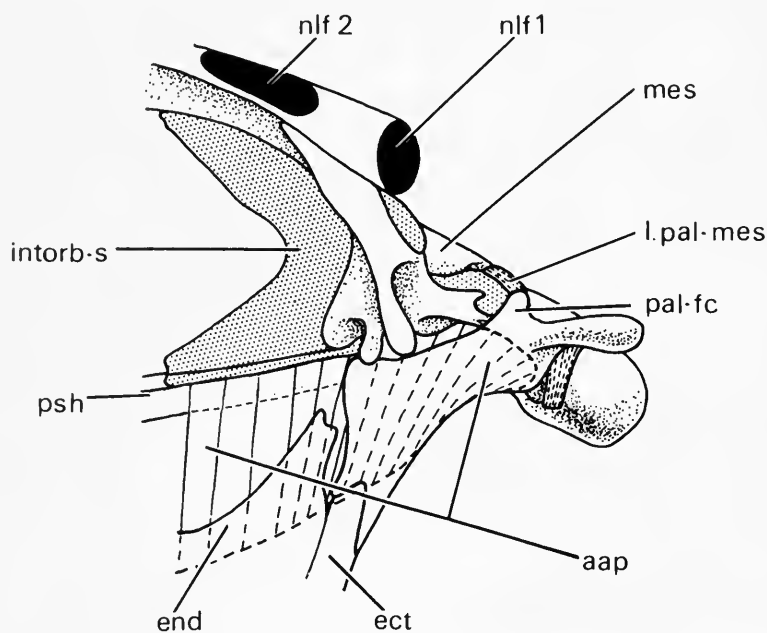
Fig. 14 Ethmovomerine region of *Trematocara unimaculatum.* The insertion area of the adductor arcus palatini muscle is indicated by broken lines.

Bathybates and other cichlid taxa (Figs 13B & 14)

The adductor of *Bathybates* is essentially similar to that of *Rhamphochromis* although as can be seen from the accompanying figure (Fig. 13B) the angle of orientation of the fibres inserting onto the palatine fossa is not as acute and the fibres pass ventrally. This seems to be a result of the position of the lateral ethmoid-palatine articulation facet which is situated more anteriorly in *Rhamphochromis*.

An arrangement similar to that of *Rhamphochromis* is present in other elongate piscivores of Lake Malawi e.g. '*Haplochromis*' *caeruleus* and '*Haplochromis*' *spilorhynchus*, and those of Lake Victoria e.g. *Prognathochromis macrognathus*, whilst one similar to that of *Bathybates* is present in other Lake Tanganyika genera e.g. *Haplotaxodon, Callochromis, Hemibates, Ectodus,* and *Aulonocranus.* Unfortunately insufficient outgroup data are available to enable the polarity of this character complex to be determined.

In *Trematocara marginatum* the arrangement is as in *Bathybates* but in the remaining species of *Trematocara* the adductor has apparently migrated anteriorly along the parasphenoid and onto the ventrolateral face of the vomer from where the fibres pass posteroventrally to insert into the palatine fossa (Fig. 14).

In common with Chichoki's (1976) observations, I have found that the adductor in all of the South American, Madagascan, and Asian species examined does not contact the medial face of the palatine and extends only as far rostrally as the medial face of the endopterygoid bone.

The levator operculi. The levator passes between the lateral neurocranial wall and the operculum, caudal to the dilatator operculi.

The levator is constant in form and position throughout the Cichlidae. It is an approximately triangular muscle with the apex situated dorsally. Origin is from the ventrocaudal region of the pterotic facet of the neurocranium, and the fibres fan out ventrally to insert on the medial face of the operculum, caudal to the site of insertion of the adductor operculi and the adductor hyomandibulae muscles. The anterior portion of the muscle inserts musculously onto the levator ledge on the medial face of the operculum, whilst the posterior fibres merge into a connective tissue sheet situated near the posterior margin of the operculum.

The adductor operculi. This cylindrical muscle connects the neurocranium with the medial face of the operculum, at a point adjacent to its articulation with the hyomandibula.

Rhamphochromis

The adductor originates musculously from the lateral region of the lateral awning (Barel *et al.*, 1976), its fibres passing laterally to insert on the adductor process which lies just behind the suspensoriad articulation socket on the levator ledge of the operculum.

No trenchant differences in the form of the adductor in *Bathybates* were recognized.

The adductor hyomandibulae. In the Cichlidae a small adductor hyomandibulae usually is present. It has apparently developed from the anterior fibres of the adductor operculi. The muscle slip originates, with the adductor operculi, from the prootic and inserts onto the medial face of the hyomandibular head adjacent to the opercular condyle of that bone.

The pharyngeal jaw apparatus (PJA)

It appears that throughout the cichlid radiation the full complement of perciform branchial muscles and bony elements of the PJA is retained and that no major changes occur in their spatial relationships to one another. However, within this configuration a seemingly endless spectrum of minor morphological variation is expressed. This is realized through differences in the relative size and robustness of the pharyngeal bones, the shape and distribution of their teeth, and through proportional changes in the various muscles coupled with slight differences in their sites of origin and insertion.

Osteological features of the PJA

The lower pharyngeal element. The lower pharyngeal element in cichlid fishes is composed of the suturally united ceratobranchials of the fifth branchial arch and their associated tooth plates. The size and shape of the resultant element, as well as the form and distribution of the pharyngeal teeth, shows considerable interspecific variation. Indeed, tooth form varies not only between taxa but also in different fields of the element in one individual. An antero-posterior gradient of increasing tooth specialization is considered as being the standard cichlid arrangement (Liem, 1978). Typically the lower pharyngeal element, which is the

largest element of the PJA, is shaped somewhat like an indented triangle with the apex lying rostrally. Posterolaterally the bone terminates, on either side, in a posteriorly directed horn (=muscular process of Liem, 1973) and a ventral keel is developed.

Liem (1973, 1978) and Liem & Osse (1975) have drawn attention to convergence in pharyngeal tooth form in trophically related groups. Amongst piscivores Liem (1978) illustrates the pharyngeal teeth of *Lamprologus compressiceps* and '*Haplochromis*' *compressiceps*, fishes which belong to distinct phyletic lineages, but which have an almost identical pharyngeal dentition.
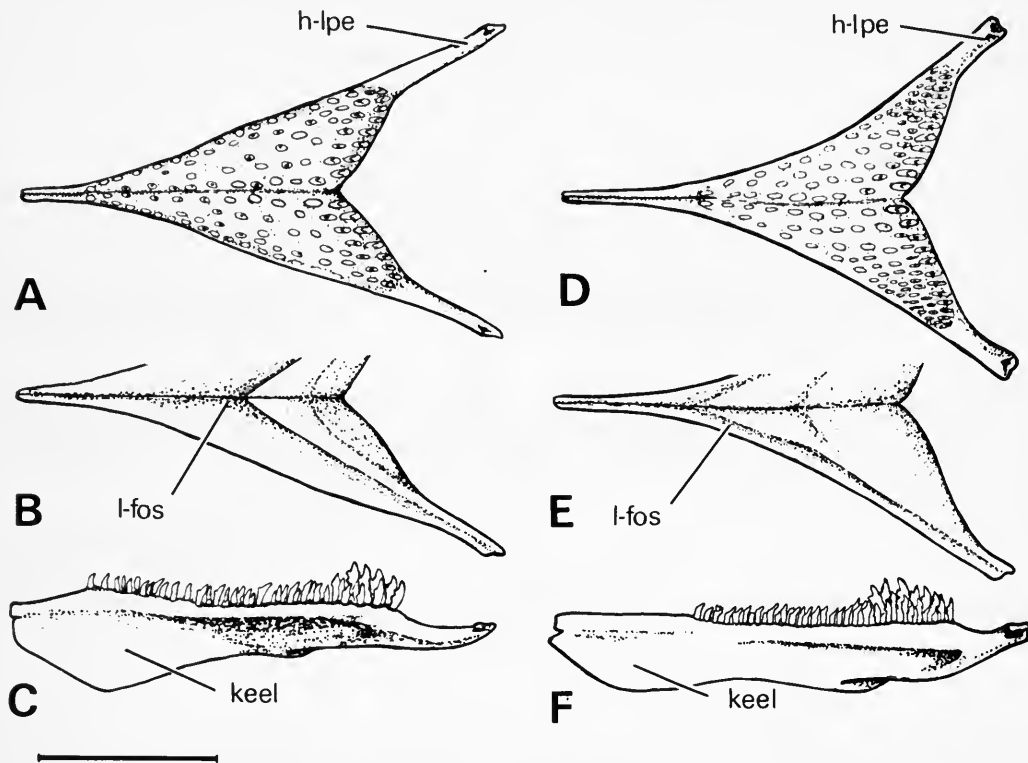
Fig. 15 Lower pharyngeal element. Left, *Bathybates ferox.* A. Dorsal view. B. Ventral view (right half). C. Lateral view. Right, *Rhamphochromis longiceps.* D. Dorsal view. E. Ventral view (right half). F. Lateral view.

Rhamphochromis

The lower pharyngeal element of *Rhamphochromis* is illustrated in Fig. 15D, E, F and as can be seen the bone is relatively elongate and is of a form commonly encountered amongst piscivorous cichlids (Poll, 1956; Greenwood, 1962, 1974; Barel, van Oijen, Witte & Witte-Maas, 1977; Hoogerhoud & Barel, 1978; Liem, 1978).

Seen ventrally, the medial region of the bone is rounded and convex and the lateral fossae are narrow. The dentigerous surface is roughly triangular in outline and the teeth are relatively fine. As in most cichlids the pharyngeal teeth located in the posterior field of the bone are the larger ones. In the anterior field the teeth are slender unicuspids in which the acutely pointed cusp is frequently directed caudally. The teeth become increasingly bevelled and the final two rows of somewhat enlarged teeth bear slightly hooked major cusps below which are a series of two to four accessory cusps. On the lower pharyngeal element these cusps are borne on the anterior edge of the teeth. It is this series of accessory cusps that gives these teeth their serrated appearance. The pharyngeal teeth are 'crowded' caudolaterally but uniformly distributed over the rest of the dentigerous surface.

Bathybates

The lower pharyngeal element is elongate and the tooth form and gradation are similar to those described for *Rhamphochromis*. A caudolateral 'crowding' of the teeth also occurs in *Bathybates* although the remaining teeth are sparsely and less uniformly arranged over the rest of the dentigerous surface. As can be seen from the accompanying illustration (Fig. 15A, B, C) the dentigerous area is enlarged and covers most of the pharyngo-buccal face of the lower pharyngeal element. In ventral view the lateral fossae are expanded and the bone is usually flattened but in some individuals it is concave.

Of the *Bathybates* species examined, *Bathybates ferox* displays the most extreme modification of the lower pharyngeal element, but all the species share an enlargement of the dentigerous area, a dorsoventral flattening of the caudal region of the bone, and an increased fossa width.

Both the enlargement of the dentigerous surface and the dorsoventral flattening of the caudal region of the pharyngeal element in *Bathybates* species are, on the basis of their limited distribution, interpreted as derived characters. The lower pharyngeal element of *Rhamphochromis* is rather typical of that found in the majority of piscivorous, elongate cichlids and no trenchant differences are recognized.

The pharyngeal dentition is similar in all of the piscivorous cichlids examined. The occurrence of this specialized tooth form amongst the piscivorous lineages in Lake Victoria (Greenwood, 1974), in *Lamprologus compressiceps* and other distantly related piscivores (Liem & Osse, 1975; Liem, 1978) seems to indicate that an independent evolution of this type of pharyngeal dentition is not uncommon amongst piscivorous cichlids. For this reason the extreme similarity in tooth form and gradation between *Bathybates* and *Rhamphochromis* is interpreted as convergence.

The upper pharyngeal jaws. As with the lower pharyngeal element, the size and shape of the constituent elements of the upper pharyngeal jaws as well as the form of their dentition, show considerable interspecific variation. Less consideration has, however, been given to the upper pharyngeal elements as a potential source of taxonomically useful characters. This is partly because of their relative inaccessability but also, since both upper and lower elements operate as a functional unit, adaptational changes in the lower element are reflected in concomitant changes in the upper elements.

Rhamphochromis (Fig. 16A)

The principal bony elements constituting the upper pharyngeal jaw in *Rhamphochromis*, in common with all cichlids, are the paired second and third* pharyngobranchials (and their associated tooth plates) and the fourth upper tooth-plate.

A pair of first pharyngobranchials (Pb1) serve to suspend the jaws from the neurocranium. Each is a stick-like ossified element connecting the anterior arm of the first epibranchial with the prootic just below the lateral commissure. The first pharyngobranchials lack associated tooth plates.

Each second pharyngobranchial (Pb2) is situated anterior to the third and is linked to the dorsomedial face of that element by a tract of connective tissue so that it lies with its caudal border closely apposed to the third pharyngobranchial (Pb3). Fused to the ventral surface of each Pb2 is a narrow, relatively elongate tooth plate with five or six teeth arranged in a single row. Each tooth bears a hooked major cusp with two accessory cusps above it. These cusps are borne on the lateral side of the teeth.

The third pharyngobranchials are the largest elements of the upper jaws. On the dorsal

The term pharyngobranchial as used in this study refers to the infrapharyngobranchial. Amongst recent teleosts, ossified suprapharyngobranchials only occur in the first arch of elopids and alepocephalids and are thus not considered.

The problem of the correct homology of the element with which the third and fourth epibranchials articulate is discussed by Ismail (1979) and Ismail & Verraes (in prep.). Throughout the present study it is assumed that this element represents the third pharyngobranchial alone.
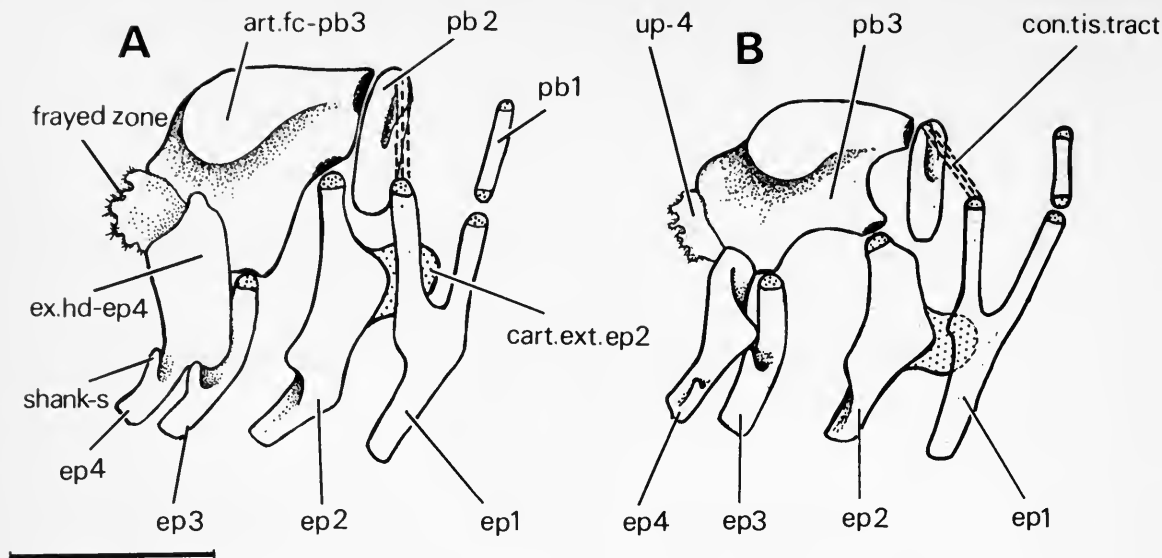
Fig. 16 Right upper pharyngeal jaw (dorsal view) in A. *Rhamphochromis longiceps* B. *Tremato-cara marginatum.*

surface of each bone there is a prominent raised facet which articulates with a corresponding process, the pharyngeal apophysis, on the base of the neurocranium (see Greenwood, 1978). Fused to the ventral surface of each Pb3 is a large tooth plate in which all the teeth have a hooked major cusp with two or three accessory cusps below it. In the caudal region the teeth become progressively smaller and more numerous.

The fourth upper tooth-plates (UP4) are well ossified and each is closely apposed to the caudal border of the corresponding Pb3. Each tooth plate bears numerous small hooked teeth also with tiny accessory cusps. Along the caudal margin of these bones there is a 'frayed zone' (the crista pharyngobranchialis of Goedel, 1974b) composed of numerous, very small, irregularly scattered unicuspid teeth. A strong connective tissue link exists between the Pb3 and UP4 of either side of the pharynx so that the whole complex apparently functions as a single unit.

Bathybates

As in *Rhamphochromis* the upper pharyngeal jaw complex as a whole is not robust and it is relatively elongate. The form and arrangement of the teeth are similar to those described in *Rhamphochromis* (see Liem, 1978 for other piscivorous cichlids).

In the course of this investigation, no trenchant differences were recognized in the form and composition of the upper pharyngeal jaws of *Rhamphochromis* and *Bathybates*. Both genera possess the typical piscivorous cichlid configuration (Hoogerhoud & Barel, 1978; Liem, 1978).

Other cichlid taxa

Of the outgroup taxa examined, all the *Trematocara* species share a characteristic feature of the third pharyngobranchial bones, *viz* the anterior margin of Pb3 is deeply indented, giving the margin a 'U'-shaped outline (Fig. 16B). This feature of Pb3 is not found in any other taxa and is assumed to be a synapomorphy uniting the species of the genus.

The epibranchial skeleton. Because of the intimacy of their association with the pharyngo-branchials, both in terms of structure and function, the epibranchials are considered as part of the upper pharyngeal jaw complex.

Barel *et al.* (1976) have produced an admirable description of the epibranchial series in

Astatotilapia elegans, and since the form of these bones in *Bathybates* and *Rhamphochromis* differ little from those of *A. elegans*, the following description will only highlight those features which are of presumed phylogenetic significance.

Rhamphochromis (Fig. 16A)

The first epibranchials (Ep1) are 'Y'-shaped elements. In each the rostral arm contacts the medial face of its respective Pb2 via a thin tract of connective tissue. An interarcual cartilage (Rosen & Greenwood, 1976) is completely absent in the majority of specimens examined. One specimen did retain a small nubble of cartilage suspended in this connective tissue tract, but the cartilage did not contact either Ep1 or Pb2.

Each second epibranchial (Ep2) contacts the dorsolateral face of Pb2 and the uncinate process contacts the anterior margin of Pb3 on its dorsolateral face. The main body of each Ep2 is rostrally expanded and the anterior margin projects medial to the uncinate process of Ep1. This expanded margin is capped with a flange of cartilage.

The third epibranchials (Ep3) are the smallest of the series. The main shaft of each contacts Pb3, and a well developed caudolateral process articulates with a corresponding facet on the fourth epibranchial.

Each forth epibranchial (Ep4) has a rostrally expanded head (the quadrangular region of Barel *et al.*, 1976). This enlarged head is slightly incurved and forms a large, posteriorly directed cupped area that overlies the dorsal face of UP4. The dorsal tip of the head of Ep4 articulates with a dorsal eminence formed at the junction of Pb3 and UP4. The rostral margin of each Ep4 bears an articulatory facet for the caudolateral process of Ep3; just below this facet the shank of Ep4 is produced into a well developed shank spine.

Bathybates

No trenchant differences in the form or arrangement of the epibranchials of *Bathybates* and *Rhamphochromis* were recognized

Other cichlid taxa

In the great majority of taxa examined the epibranchials are of the form described above. However, amongst the Lake Tanganyika genera all species of *Trematocara* possess a characteristically shaped Ep4 (Fig. 16B). In these fishes the head of Ep4 is not expanded or cupped, and the shank spine is reduced in size. The absence of this expanded head in *Trematocara* is interpreted as a secondary loss within the family rather than as the retention of the plesiomorphic perciform condition. It has been suggested elsewhere (page 77) that *Trematocara* is the sistergroup of *Hemibates* and that together these two form the sistergroup of *Bathybates*. A typical cichlid expansion of the head of Ep4 is present in both *Hemibates* and *Bathybates*. It must be assumed therefore that the ancestor of the whole group possessed an Ep4 with an expanded head. If this was the case then the expansion must have been secondarily lost in *Trematocara* species.

Myological features of the PJA

The dorsal branchial muscles develop from the muscle plates which are formed in each of the branchial segments, and may be grouped according to their developmental origin and innervation (Edgeworth, 1935).

Group one muscles

The levatores externi muscles. The four pairs of levator externus muscles connect the neurocranium with the four pairs of epibranchials and the lower pharyngeal element. They originate, together with the levatores interni, as a single muscle mass from the hyomandibulad shell of the neurocranium.
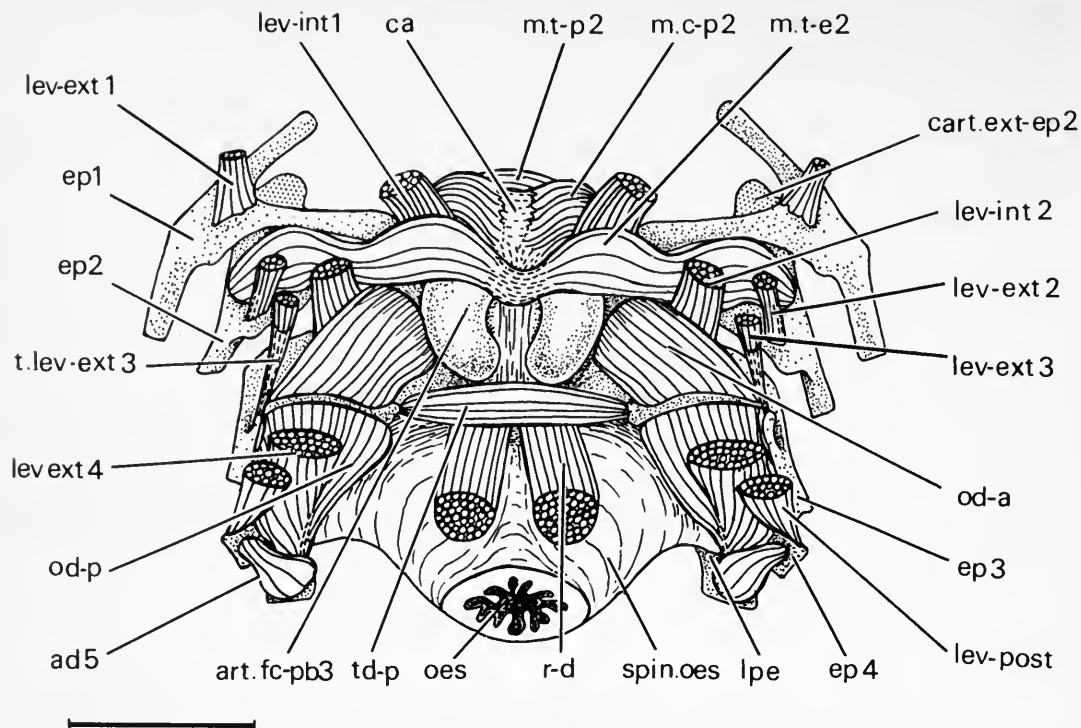
Fig. 17 *Rhamphochromis longiceps,* dorsal view of isolated pharyngeal jaw apparatus.

Rhamphochromis (Fig. 17)

FIRST LEVATOR EXTERNUS. This rostral levator passes caudoventrally from the hyomandibulad shell to insert musculously onto the dorsal face of Ep1. The insertion site is quite extensive and is situated on the dorsomedial face of Ep1 at the junction of its rostral and caudal arms.

SECOND LEVATOR EXTERNUS. This muscle originates, with the first levator, from the rostral part of the lateral rim of the hyomandibulad shell. It inserts onto the dorsolateral face of Ep2 at a point just above the triangular edge of the caudal border of that bone. The anterolateral fibres are tendinously associated with Ep2; the remaining fibres insert musculously.

THIRD LEVATOR EXTERNUS. This is the smallest of the series and is closely apposed to the rostrolateral side of the fourth levator for its entire length. It terminates in a long tendon which inserts onto the tip of the caudolateral process of Ep3.

FOURTH LEVATOR EXTERNUS. This is the largest of the levator series. The lateral section originates from the lateral rim of the hyomandibulad shell, the remaining section originating behind the levatores interni from the medial part of the shell. The two sections merge ventrally to form a single muscle mass. A small slip of lateral fibres inserts, via a short tendon, onto the well developed shank spine. The mass of the levator bypasses the shank spine, passing medial to it, and tapers onto a tendon which inserts on the horn of the lower pharyngeal element medial to the insertion of the fifth adductor muscle.

Bathybates (Fig. 18)

The levatores externi series of *Bathybates* is similar to that of *Rhamphochromis.* However, in *Bathybates* the third levator inserts onto a small aponeurosis and a long tendon is not developed.

Other cichlid taxa

In other cichlids the mode of insertion of the first three levatores externi is as described for

Rhamphochromis. The elongation of the tendon of the third levator externus in *Rhamphochromis longiceps* (and to a lesser extent that of the other *Rhamphochromis* species) is unusual although the length of this tendon in some other species, for example *Prognathochromis prognathus* from Lake Victoria, does approach the *Rhamphochromis* condition.

In the majority of taxa examined the third levator externus inserts onto Ep3 via a well developed, but not elongate, tendon. The reduction of this tendon, like that in *Bathybates*, is also found in other Lake Tanganyika genera, for example *Hemibates, Trematocara, Lamprologus, Limnochromis, Aulonocranus,* and *Ctenochromis*. Insufficient data on the distribution of various character states of the third levator insertion are available to permit interpretation of polarity in the character at an intergeneric level.

According to Liem & Osse (1975) and Liem (1978) the fourth levator externus in all cichlid fishes is composed of a small strap-like lateral head inserting onto the shank spine of Ep4, and a large medial head which passes medial to the spine to insert tendinously onto the posterior horn of the lower pharyngeal element. It was this shift in the major insertion site of the fourth levators (from the fourth epibranchials to the lower pharyngeal element) that Liem (1973) considered to be part of the 'key innovation' of the Cichlidae.

In *Trematocara* the fourth levator externus does not retain an attachment on Ep4 and the entire muscle passes over the head of Ep4 to insert tendinously on the horn of the lower pharyngeal element. The loss of a lateral section inserting onto Ep4 is interpreted as a synapomorphy uniting the species of the genus.

The levator posterior muscle. According to Edgeworth (1935) the levator posterior represents a fifth levator externus that has migrated caudally to originate from the ventrolateral face of the pterotic region of the neurocranium.

The levator posterior is separated from the rostral levators by a hiatus within which the adductor operculi muscle is situated.

Rhamphochromis (Fig. 17)

The fibres of this large muscle pass ventrocaudally from their origin on the ventral face of the pterotic and intercalar bones to insert musculously on the dorsolateral margin of Ep4 and the dorsal border of the shank spine. Some ventromedial fibres intercalate with the dorsal fibres of the medial section of the fourth levator externus.

Bathybates (Fig. 18)

The origin of the levator posterior is situated further medially in *Bathybates* than in *Rhamphochromis,* and is restricted to the intercalar bone.

Other cichlid taxa

In the majority of cichlid taxa examined the levator posterior originates from the ventrolateral region of the lateral awning, usually from the pterotic and intercalar bones (see Hoogerhoud & Barel, 1978).

In *Hemibates* the origin of the levator has migrated medially onto the exoccipital bone at a site just anterior to the vagus foramen. This shift in origin does not appear to be correlated with the presence of an inflated otic bulla since in *Aulonocranus*, another genus with an inflated bulla, the origin of the levator is in the usual position. Similarly in *Trematocara* although the origin of the levator is more medially situated than in *Rhamphochromis* it is still restricted to the lateral awning.

The medial migration of the levator posterior in *Hemibates* is interpreted as the derived condition and it represents the end point of a trend visible in both *Bathybates* and *Trematocara*.

The levatores interni muscles. The two pairs of levatores interni muscles originate, together
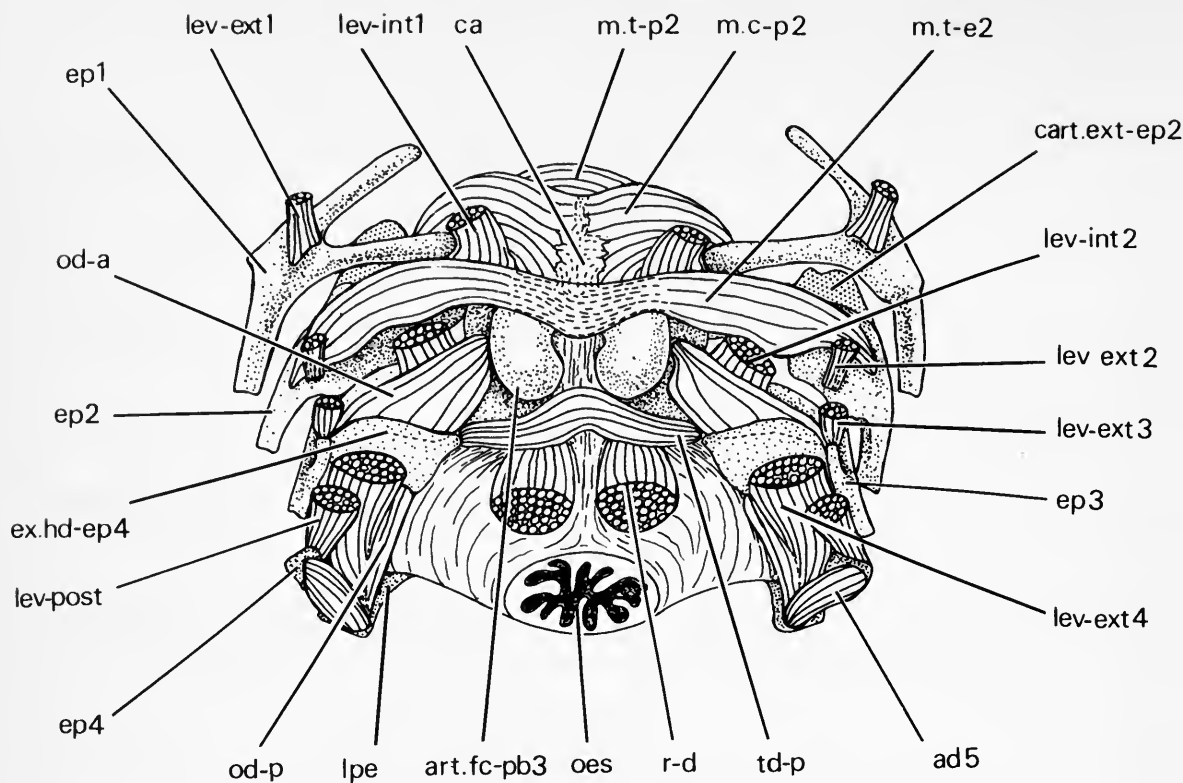
Fig. 18 *Bathybates ferox,* dorsal view of isolated pharyngeal jaw apparatus.

with the levatores externi 1–3, from the hyomandibulad shell between the lateral and medial sections of the fourth levator externus.

Rhamphochromis (Fig. 17)

FIRST LEVATOR INTERNUS. This rostral levator originates on the hyomandibulad shell medial to the second levator internus. It is a relatively large muscle that passes ventrally (and slightly caudally) and tapers into a short aponeurosis that inserts on the dorsomedial junction of Pb2 and Pb3 just caudal to the uncinate process of Ep1.

SECOND LEVATOR INTERNUS. The second levator is slightly pinnate and originates lateral to the first levator internus. Fibres pass ventrocaudally to insert via a short aponeurosis onto the ventrolateral face of Pb3 just anterior to the head of Ep3.

Bathybates (Fig. 18)

The levatores interni have similar sites of origin and insertion to those described above for *Rhamphochromis.* The first levator inserts musculously and is slightly expanded at its base.

Other cichlid taxa

The size of the levatores interni varies considerably amongst cichlid fishes (see Liem & Stewart, 1976). Hoogerhoud & Barel (1978) interpret the relatively large levatores interni of piscivorous species to be part of a complex of adaptations associated with the trituration of prey.

Insufficient outgroup data render ambiguous any phylogenetic interpretation of the differences between the insertion of the first levator internus in *Rhamphochromis* (via a short aponeurosis) and that in *Bathybates* (musculously).
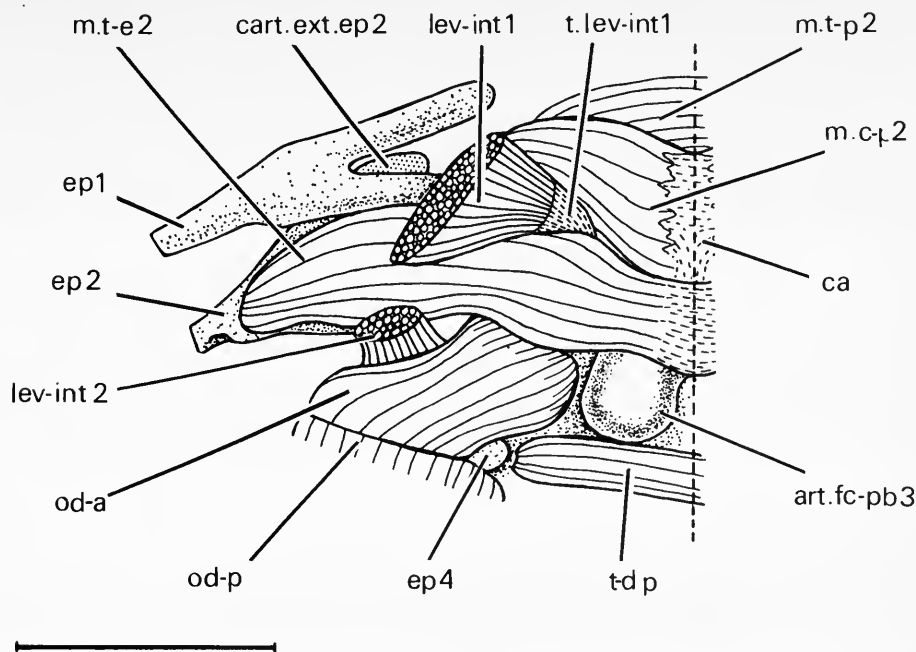
Fig. 19 *Trematocara marginatum*, dorsal view of anterior region of isolated pharyngeal jaw apparatus (left side).

In *Hemibates* and *Trematocara* (Fig. 19) the first levator internus muscles are rostrocaudally expanded and insert via well developed strap-like tendons. The rostrocaudal expansion of the first levator occurs in other species with inflated otic bullae eg. *Aulonocranus* and *Aulonocara* (cf. Hoogerhoud & Barel, 1978) but the presence of a well developed strap-like tendon is not so correlated. It is therefore assumed that this strap-like tendon is a synapomorphy shared by *Trematocara* and *Hemibates*.

The adductores muscles. *Rhamphochromis*

With the exception of the fifth muscle the adductores are situated in the angle between the dorsal part of the ceratobranchial and the shank of the epibranchial of each arch. The fifth adductor is the caudal representative of the series whose site of attachment has shifted onto Ep4 with the loss of Ep5. The fifth adductor is spindle shaped and it passes from the shaft of Ep4 at a point below the shank spine to insert onto the horn of the lower pharyngeal element. A few ventromedial fibres intercalate with those of the fourth levator externus.

No trenchant differences in the adductor series of *Bathybates* were recognized

Group two muscles

The remaining muscles of the dorsal gill arches are all derived from the sphincter oesophagi (Edgeworth, 1935) which is itself a derivative of the upgrowth around the oesophagus of the ventral ends of the muscle plates of the fifth branchial arch (Holstvoogd, 1965). All these muscles are innervated by branches of the vagus nerve (Edgeworth, 1935).

The sphincter oesophagi. The sphincter oesophagi forms a continuous muscle sheath around the oesophagus. No separate muscle bundle crosses the dorsal midline anterior to the entrance of the retractor dorsalis into the oesophageal tissues.

The transversi dorsales muscles
Rhamphochromis (Fig. 17)

As in all cichlids there are two distinct parts of this muscle, the transversus dorsalis anterior and posterior.

The transversus dorsalis anterior is a large tripartite muscle. The anterior part (the musculus transverus pharyngobranchialis 2 of Anker, 1978) is a relatively small, well defined muscle. It arises from the lateral part of the rostral face of Pb2 and its fibres pass medially across the midline to attach to the Pb2 of the opposite side.

The second part of this muscle complex (the musculus cranio-pharyngobranchialis 2 of Anker, 1978) connects the second pharyngobranchials with each other as well as with the neurocranium. The anterior fibres pass medially and insert on a complex median aponeurosis which in turn is attached to the parasphenoid bone at the base of the pharyngeal apophysis. The bulk of the muscle passes caudomedially to join the central aponeurosis of the third part of the muscle and the fibres of the opposite side.

The third part (the musculus transversus epibranchialis 2 of Anker, 1978) originates from the dorsal face of Ep2; its fibres pass medially to insert on a flat, strip-like aponeurosis which traverses the anterior face of the articulatory facets of the third pharyngobranchials.

The transversus dorsalis posterior (the musculus transversus epibranchialis 4 of Anker, 1978) is separated from the anterior muscle complex by a hiatus so that the articulatory facets of the third pharyngobranchials are exposed to form a diarthrosis with the pharyngeal apophysis. The strap-like transversus dorsalis posterior originates from the caudal eminence formed at the junction of Pb3 and UP4. The fibres pass medially and are not interrupted by a central aponeurosis.

Bathybates (Fig. 18)

The arrangement of this muscle complex is similar to that just described. However, the musculus cranio-pharyngobranchialis 2 is considerably larger in *Bathybates* than is its counterpart in *Rhamphochromis*. This is also the case in other Lake Tanganyika genera, whilst in other Lake Malawi genera and in the riverine *Serranochromis* the muscle proportions are as described in *Rhamphochromis*. Unfortunately too few outgroup data preclude any phylogenetic interpretation of these differences.

The obliqui dorsales muscles. Winterbottom (1974) discusses the nomenclatural confusion that has centred around the muscles connecting the posteromedial face of Ep4 and the dorsal tip of the fifth ceratobranchial. It is considered that, with the loss of the fifth pharyngobranchial, the obliquus posterior represents a part of the obliquus dorsalis whose medial site of attachment has shifted to Ep4.

Rhamphochromis (Fig. 17)

The obliquus dorsalis anterior is a well developed muscle. It originates from the lateral wall of the articulatory facet of Pb3 and its fibres pass caudomedially to insert along the inner face of the expanded head of Ep4. Some fibres also insert along the caudolateral process of Ep3.

The obliquus dorsalis posterior is also well developed. It connects the expanded head of Ep4 with the horn of the lower pharyngeal element. The fibres of the obliquus posterior insert onto the tendon of the fourth levator externus, and together these two muscles insert tendinously on the horn.

Bathybates (Fig. 18)

The obliquus posterior is markedly reduced and is represented by a small strand of fibres originating from the dorsomedial face of the head of Ep4; as a result most of the head of that bone is exposed.

Other cichlid taxa

Liem (1978:346) states that '. . . the obliquus posterior is either weakly developed or absent in piscivorous cichlids.' Observations made during the course of this study contradict that assessment. For example in the *Rhamphochromis, Boulengerochromis, Serranochromis, Lamprologus*, and *Hemibates* species examined, as well as in '*Haplochromis*' *caeruleus*, '*Haplochromis*' *dimidiatus*, '*Haplochromis*' *woodi* and *Prognathochromis prognathus*, many

of which species were studied by Liem, an obliquus posterior is present and is not markedly reduced.

On the basis of these data, as well as the widespread occurrence of a well developed obliquus posterior in the majority of taxa from other trophic groups, the reduced area of origin and total size of the obliquus posterior in *Bathybates* is interpreted as a derived character.

The retractor dorsalis muscles. The bilaterally paired muscles connect the posterior pharyngobranchial elements with the vertebral column. The size of the retractor varies markedly within the Cichlidae (Hoogerhoud & Barel, 1978) and the site of origin is from the ventral face of the anterior vertebrae and includes the apophysis that is developed on the third, fourth or fifth abdominal vertebrae (Trewavas, 1964; Greenwood, 1979).

Rhamphochromis (Fig. 17)

The retractor originates from the ventrolateral face of the first, second, and third abdominal vertebrae and from the ventral apophysis on the third vertebra. Its fibres pass rostro-ventrally and insert musculously as two distinct bundles on the mediocaudal face of the third pharyngobranchials; a few fibres insert on the rostral region of UP4.

No trenchant differences in the retractor of *Bathybates* were recognized.
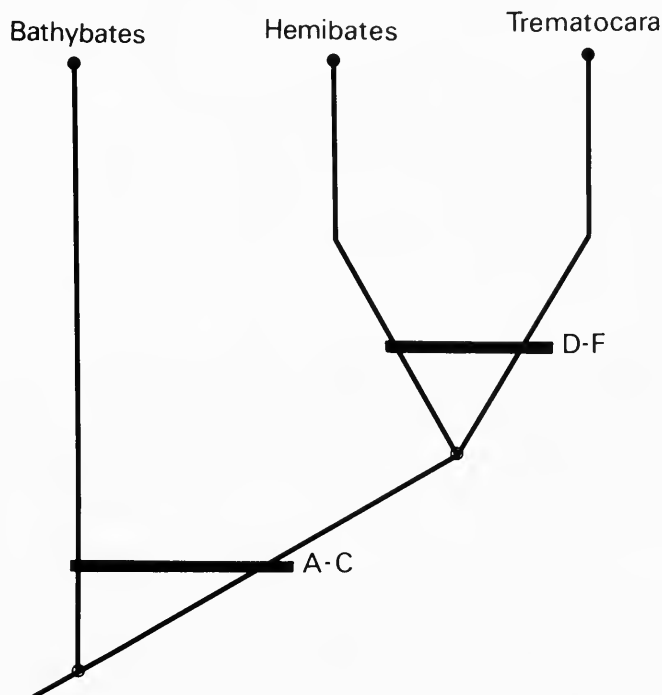
Fig. 20 Cladogram illustrating the hypothesis of relationship for *Bathybates*. Apomorphic characters defining the genera *Bathybates, Hemibates* and *Trematocara* are discussed in the text (see Stiassny, 1980 for additional data). Synapomorphies: A. Laterally expanded ascending process of the anguloarticular. B. Palatine-lateral ethmoid ligament absent. C. The dorsal bony bridge reduced or absent. D. Tendon of the first levator internus broad and strap-like. E. Palatine-mesethmoid ligament present. F. Elongate rostral cartilage extending below the articular processes of the premaxillae.

Discussion

A number of apomorphic characters has been identified amongst the cichlid taxa studied and on the basis of these features it is possible to establish the monophyly of *Bathybates* and to generate an hypothesis of phylogenetic relationships for that genus (Fig. 20).

The relatively high degree of morphological differentiation exhibited by the Lake Tanganyika Cichlidae renders that flock a most suitable subject for cladistic analysis at the intergeneric level. This was not found to be the case with the Lake Malawi Cichlidae.

Although the range of morphological differentiation throughout the whole flock is greater in Lake Malawi than in Lake Victoria, with respect to the piscivorous species at least, a similar situation exists in the two lakes. The range of morphological variation amongst the various taxa is narrow and in most cases if structures are simply regarded in terms of presence or absence no character differences are distinguishable. In this respect Greenwood's (1974) conclusion that the different characteristics identified in the Lake Victoria '*Haplochromis*' flock are but slight variants of a basic 'bauplan' developed and differentiated by ontogenetic reorganization, may be broadened to include the piscivorous grade of Lake Malawi. This is not to imply that a close phylogenetic relationship exists between the Lake Victoria and Lake Malawi haplochromines or that the Lake Malawi piscivores are necessarily a phylogenetic lineage.

None of the character complexes investigated in the preceding sections has revealed apomorphic character states in *Rhamphochromis*. Although all of the species currently included in this genus do have a highly distinctive 'facies' such an overall similarity does not, in itself, constitute evidence of monophyly.

Given the extreme appearance of these *Rhamphochromis* species it is surprising that very few apomorphic characters can be found to define the genus.

Regan (1921) was of the opinion that the beak-like expansion of the premaxillae (Fig. 6A) characterized the genus, but similar premaxillary expansion is also present in '*Haplochromis*' *caeruleus*, '*Haplochromis*' *strigatus*, and '*Haplochromis*' *compressiceps* from Lake Malawi as well as in some Lake Victoria piscivores. Regan also noted that the anterior teeth of the second series in the upper jaw are enlarged in *Rhamphochromis* species. This feature does appear to characterize all the species of *Rhamphochromis*. In all *Rhamphochromis* species the urohyal bone lacks an anterodorsal process. In the great majority of other cichlid species the urohyal bears a distinct anterodorsal spine (Barel *et al.*, 1976) and thus its presence is interpreted as a plesiomorphic character within the Cichlidae. *Rhamphochromis* is unique amongst Lake Malawi Cichlidae in lacking this spine. The loss of the spine occurs mosaically amongst the Lake Tanganyika genera and therefore is assumed to have taken place independently a number of times within that lake. All of the Lake Victoria taxa examined have an anterodorsal spine on the urohyal.

All *Rhamphochromis* are large, elongate, streamlined fishes and similar features also characterize the piscivorous grade of Lake Victoria '*Haplochromis*' (Greenwood, 1962, 1974). In Lake Victoria body elongation is not accompanied by a marked increase in the total number of vertebrae. The range of vertebral counts for these species is 30–32, whilst that of the more 'generalized' forms is 27–30 (Greenwood, 1962; Greenwood & Barel, 1978). This slight increase in total number involves an increase in the number of caudal, rather than abdominal vertebrae (Greenwood, 1979).

Amongst the piscivores of Lake Malawi an increase in size and elongation of the body is frequently accompanied by an increase in the total number of vertebrae, and many species have a higher total count than their Lake Victoria counterparts. For example; '*Haplochromis*' *strigatus* 30–32 (13–14 + 17–18), '*Haplochromis*' *dimidiatus* 32–33 (13–14 + 18–20), '*Haplochromis*' *caeruleus* 34 (15 + 19), '*Haplochromis*' *spilorhynchus*, 33–34 (15 + 17–18), '*Haplochromis*' *lepturus* 33–35 (15–16 + 18–19), '*Haplochromis*' *macrostoma* 31–32 (13–14 + 17–18), '*Haplochromis*' *compressiceps* 31–32 (13–14 + 17–18), *Aristochromis christyi* 32 (14–15 + 17–18), *Diplotaxodon argenteus* 33 (16 + 17).

Rhamphochromis stands alone amongst the Lake Malawi Cichlidae in possessing a much

higher total number of vertebrae (as many as 39 in some specimens of *Rhamphochromis leptosoma*). Furthermore, *Rhamphochromis* is easily distinguished from the other Lake Malawi (and Lake Victoria and Lake Tanganyika) cichlids by the fact that the increase in the total number of vertebrae involves an increase in the number of abdominal vertebrae. In all species of *Rhamphochromis* the number of abdominal vertebrae is 17 or more.

This increase in the total number of vertebrae, and the increase in the number of abdominal vertebrae, are both interpreted as apomorphic characters which serve to distinguish *Rhamphochromis* from other Lake Malawi haplochromines. But as can be seen from the figures given above '*H.*' *caeruleus*, '*H.*' *spilorhynchus* '*H.*' *lepturus, Aristochromis* and *Diplotaxodon* display a slight increase in the number of abdominal vertebrae, and a similar, though more marked increase is found in the members of the *Serranochromis* lineage (Greenwood, 1979; Trewavas, 1964; Bell-Cross, 1975).

Greenwood (1979) has suggested that *Serranochromis* may have contributed to the Lake Malawi flock; the shared apomorphic character of an increased number of abdominal vertebrae found in *Serranochromis* and *Rhamphochromis,* and to a lesser extent, also in '*H.*' *caeruleus*, '*H.*' *spilorhynchus* '*H.*' *lepturus, Aristochromis* and *Diplotaxodon* may reflect a close relationship amongst these fishes.

In many ways *Rhamphochromis* represents an endpoint in an evolutionary trend towards the production of a highly specialized morphotype. Though often extreme, the characters involved in the production of this large mouthed, streamlined fish are linked through a gradal series to those found in the less modified piscivores of Lakes Malawi and Victoria. From a knowledge of intra- and interspecific variation in meristic characters, neurocranial and dental morphology, and from ecological and biological data for much of the Lake Victoria flock, Greenwood was later able to breakdown the piscivorous grade into two phyletic lineages (1980). Unfortunately, comprehensive data of this nature are not available for the majority of the Malawi Cichlidae and in their absence a similar breakdown of the Malawi piscivores cannot be achieved.

The level of discrimination provided by this purely anatomically based cladistic investigation has proven to be adequate when applied to an intergeneric analysis of the Lake Tanganyika cichlids but insufficient to detect salient character differences within the Lake Malawi flock. It seems that in the face of low morphological differentiation combined with a high level of species proliferation, a cladistic approach relying upon purely anatomical data is stretched to its limits. If the phylogenetic relationships of *Rhamphochromis* and the other Lake Malawi cichlids are to be resolved then ecological, ethological and possibly physiological characters must be employed within the same framework (see also Greenwood, 1980).

Acknowledgements

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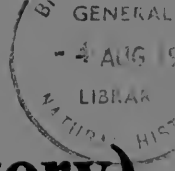Eugène Penard's Slides of Gymnamoebia: re-examination and taxonomic evaluation. By F. C. Page

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The calceolus, a sensory structure of gammaridean amphipods (Amphipoda: Gammaridea)

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Introduction

The calceolus is a microscopic external surface structure, presumed to serve a sensory function, found on the antennae of a select group of amphipods belonging to the suborder Gammaridea. It occurs in only about 10 per cent of the known gammaridean species, and is absent elsewhere in the Crustacea. First noted by Milne-Edwards in 1830 and referred to as the 'cupule membraneuse', it later acquired the name 'calceolus' because of its slipper-shaped profile when viewed under a microscope. A good account of contemporary knowledge was provided by Blanc (1883, 1884).

Despite this early recognition, calceoli have since received only limited attention from taxonomists and physiologists, and remain largely enigmatic inconsistently-documented structures. Their occurrence is uncertain in many species, they are poorly understood in terms of morphology and ontogenetic development, and their precise function has yet to be established. The small size of calceoli (20–300 μm) is the probable explanation for this lack of attention, since good resolution of their intricate surface structure is almost impossible using conventional light microscopy, and they are easily overlooked at the lower magnifications often used in figuring antennae for taxonomic work. A few attempts have been made by taxonomists to draw calceoli at high magnification under a light microscope, and some idea of the general profile and surface pattern has been obtained, but the true three-dimensional complexity of the structure cannot be appreciated. Some of the earliest drawings of calceoli are as good as or better than most illustrations in recent literature.

Calceoli have not always been reliably distinguished from aesthetascs. These also occur frequently on amphipod antennae but have a much simpler structure. Confusion has been especially noticeable in taxonomic work on freshwater amphipods which may have aesthetascs of unusually large size. Unlike calceoli, aesthetascs are found widely throughout the Crustacea, and are thought to function as chemoreceptors. Aesthetascs in amphipods generally have a very simple spatulate shape and are restricted to the flagellum of antenna 1. The structurally more bizarre calceoli are found on antenna 2 or both antenna 1 and 2, but not on antenna 1 alone. In some species, as for example *Eusirus antarcticus* Thomson, calceoli and aesthetascs occur together on the flagellar articles of the same individual dispelling any thoughts that calceoli and aesthetascs might simply be variants of the same surface structure. In *E. antarcticus* the calceolus is about one-third the length of the aesthetasc.

We have assembled a considerable amount of data on the occurrence and distribution of calceoli amongst amphipods but have found surprisingly little ecological or biological pattern in this information. For certain, calceoli do not occur outside the suborder Gammaridea, but of the 80 or so families of gammarideans presently recognised only 19

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Table 1 *Superfamilies and families of gammaridean amphipods* (after Bousfield, 1978). Calceoliferous families are shown in bold capital letters.

Phoxocephaloidea
  PHOXOCEPHALIDAE
  UROTHOIDAE
  PLATYISCHNOPIDAE

Lysianassoidea
  LYSIANASSIDAE

Pontoporeioidea
  HAUSTORIIDAE
  PONTOPOREIIDAE

Gammaroidea
  GAMMARIDAE
  ACANTHOGAMMARIDAE
  ANISOGAMMARIDAE
  MESOGAMMARIDAE
  Gammaroporeiidae
  Macrohectopidae
  Typhlogammaridae
  Pontogammaridae

Crangonyctoidea
  CRANGONYCTIDAE
  NEONIPHARGIDAE
  PARAMELITIDAE

Niphargoidea
  Niphargidae

Bogidielloidea
  Bogidiellidae

Eusiroidea
  EUSIRIDAE
  PONTOGENEIIDAE
  CALLIOPIIDAE
  GAMMARELLIDAE
  AMATHILLOPSIDAE
  Bateidae
  Paramphithoidae

Oedicerotoidea
  OEDICEROTIDAE

Leucothoidea
  Pleustidae
  Laphystiopsidae
  Amphilochidae
  Leucothoidae
  Anamixidae
  Maxillipiidae
  Colomastigidae
  Pagetinidae
  Nihotungidae
  Stenothoidae
  Cressidae
  Thaumatelsonidae

Talitroidea
  Hyalidae
  Hyalellidae
  Talitridae
  Ceinidae
  Dogielinotidae
  Najnidae
  Eophliantidae
  Phliantidae
  Temnophliantidae
  Kuriidae

Stegocephaloidea
  Stegocephalidae
  Acanthonotozomatidae
  Ochlesidae
  Lafystiidae

Pardaliscoidea
  Pardaliscidae
  Stilipedidae
  Hyperiopsidae
  Astyridae
  Vitjazianidae

Liljeborgioidea
  Liljeborgiidae
  Sebidae
  Salentinellidae

Dexaminoidea
  Atylidae
  Anatylidae
  Lepechinellidae
  Dexaminidae
  Prophliantidae

Ampeliscoidea
  Ampeliscidae

Melphidippoidea
  Melphidippidae

Melitoidea
  Hadziidae
  Melitidae
  Carangoliopsidae

Corophioidea
  Photidae
  Isaeidae
  Ischyroceridae
  Ampithoidae
  Biancolinidae
  Aoridae
  Cheluridae
  Corophiidae
  Podoceridae

contain calceoliferous species (Table 1), and these are restricted to just 7 of the 19 super-families (as proposed by Bousfield (1978) in a recent revision of the group). Even within these families the calceoli are far from uniformly distributed; some genera are entirely non-calceoliferous, others have both calceoliferous and non-calceoliferous species. Ecologically, the calceoliferous species show no special pattern—they may occur in marine, brackish water or freshwater (including hypogean) habitats, from shallow to abyssal depths, in polar, temperate or tropical regions, and may be active swimmers, or burrowers, or live in algae. We could find no obvious correlation of the presence or absence of calceoli with behavioural patterns. An additional dimension of variability is suggested by recent ecological work which affirms that calceoli may be present or absent in different populations of the same species, or from different samples of the same population taken at different seasons of the year (Minkley & Cole, 1963; Cole, 1970; Goedmakers, 1972; Croker & Gable, 1977), although we have

some reservations as to the universality of these statements. Jazdzewski (1977) suggests that other considerations such as the appearance of calceoli only in males of a certain age may also account for apparent variability of occurrence within species' populations.

A checklist of all known calceoliferous amphipod species is given in a recent paper by Hurley (1980). This tabulation includes only those species that have actually been described or figured in the literature as having calceoli, excluding any that are calceoliferous by inference alone (e.g. generic diagnosis). The list comprises 584 species and subspecies belonging to 134 different genera, from an estimated 5000 species and an estimated 1000 genera in the Gammaridea as a whole. Within the 19 calceoliferous families, of approximately 375 genera and 2000 species, the proportion of species possessing calceoli is a little less than one-third.

Hurley's compilation shows up some trends in the location of the calceoli on the antennae in the different families. In haustoriids, phoxocephalids and lysianassids, only the male has calceoli which may occur on antenna 1 and antenna 2, although in lysianassids they are absent from peduncular articles. Gammarids, acanthogammarids, anisogammarids and mesogammarids have a few species with calceoliferous females, but calceoli are typically restricted to the flagellum of antenna 2 in males. The crangonyctids have a similar pattern to the 4 gammaroid families above except that the calceoli occur on the peduncle as well as the flagellum of antenna 2. Eusiroids (Eusiridae, Pontogeneiidae, Calliopiidae, Gammarellidae, Amathillopsidae) are commonly calceoliferous in both sexes and on both antennae.

The function of calceoli has received very little direct attention and is far from resolved. They have variously been considered organs for clasping, copulation, and taste, and more recently linked with pheromone reception (Dahl *et al.,* 1970) but only the latter hypothesis is supported by direct experimental evidence. However, from structural and other evidence we would argue against a chemosensory role for calceoli. We believe the structural complexity of the calceoli involves some form of sound, vibration or pressure wave sensitivity.

Scanning electron microscopy was used to examine the calceoli of more than 60 different amphipod species in some 40 genera representing most of the calceoliferous families. We looked first at the morphology of a wide range of calceoli and applied this information to the problem of function. An unexpected bonus, following from the recognition of distinct structural designs amongst the calceoli, has been the rewarding prospect of using them as indicators of phylogenetic affinity.

Material and methods

All the scanning work for this study was carried out in the E.M. Unit of the British Museum (Natural History) using either a Cambridge 2A or a Stereoscan 600. Satisfactory results were obtained with antennal preparations that were simply oven dried before coating, although this was later replaced by routine critical point desiccation followed by sputter coating with gold. A variety of different methods for fixing preparations to stubs were tried and most proved adequate, but use of a thin film of Araldite was eventually adopted as the simplest and most effective. All source material from which dissections were made came either from the collections of the BM(NH) or from the N.Z. Oceanographic Institute. Some of this material had been in preservative for many years and had rather too much attached debris for high resolution photomicrography, but in all instances the basic configuration of the calceolus was quite clear, and material preserved in spirit for over a century still gave useful, if not spectacular, results.

Results

The calceoli of the sixty or so species examined showed considerable morphological diversity from the relatively simplistic condition found in *Phoxocephalus* and *Urothoe*, to

the highly complex structures in *Eusirus, Amathillopsis, Chosroes,* and others. Despite this architectural variety, a certain basic design was evident throughout.

The typical calceolus (Figs 1a, 3a) has two surface components, which we have designated the *proximal* (p.e.) and *distal elements* (d.e.), more or less closely attached to the basal *receptacle* (r.), and a slender *stalk* (st.). The *distal element* is characterised by a series of ridges or annulations, or may comprise a number of separate or partially overlapping plates. The *proximal element*, in contrast, is a single component, either a concave crescent-shaped plate closely applied to the proximal margin of the distal element, or a discrete circular cup that sits freely on the receptacle attached only by a narrow base.

In the majority of calceoli examined, except those of phoxocephalids, urothoids and crangonyctids, there is a large bulbous swelling or *bulla* (b.) at the proximal end of the receptacle close to the attachment of the stalk. In a few of the eusirid calceoli studied the proximal element had been dislodged during the preparation revealing a circular opening in the receptacle through which the base of the proximal dish appeared to connect to the underlying bulla.

Within our sample we have been able to recognise just 9 distinct structural types, and have described and illustrated each of these nine different designs, and listed those species allocated to each group. The 9 categories are designated after the significant family component; gammarid, bathyporeid, lysianassid, pontogeneiid, eusirid, gammarellid, oedicerotid, phoxocephalid and crangonyctid.

1. Gammarid (Fig. 1a–c)
    Gammarus duebeni Liljeborg
    Gammarus locusta (L.)
    Gammarus pulex (L.)
    Eulimnogammarus fuscus (Dybowsky)
    Eulimnogammarus verrucosus (Gerstfeldt)
    Echinogammarus veneris (Heller)
    Eogammarus confervicolous (Stimpson)
    Odontogammarus calcaratus (Dybowsky)
    Micruropus talitroides (Dybowsky)
    Micruropus vortex (Dybowsky)
    Micruropus wahli (Dybowsky)

The gammarid calceolus represents one of the simplest configurations. The proximal element forms a weakly concave crescentic plate closely applied along its inner margin to the distal element. The distal element usually has well defined transverse banding ranging from an observed maximum of 25–30 bands in *Eulimnogammarus verrucosus* and *Eogammarus confervicolous*, through 10 in *Micruropus wahli* to as few as 2–3 poorly defined bands in *Micruropus vortex* and *M. talitroides*. High magnification of the distal element reveals that the banded markings are not simple ridges but a series of closely overlapping transverse plates, typical of the distal elements of almost all calceoli investigated.

Gammarid calceoli are usually confined to males, are typically few in number, and there is only one calceolus on each flagellar article.

2. Bathyporeid (Fig. 1d)
    Bathyporeia guilliamsoniana (Bate)
    Bathyporeia pilosa Lindström
    Bathyporeia sarsi Watkin
    Zaramilla kergueleni Stebbing

The bathyporeid calceolus is basically similar to the gammarid-type but is characterised by short tentacle-like projections along the posterior margin of the proximal element. The proximal element is a quite small shallow crescent shaped plate in close contact with the banded distal element. The banding is very much as in the gammarid pattern, and varies
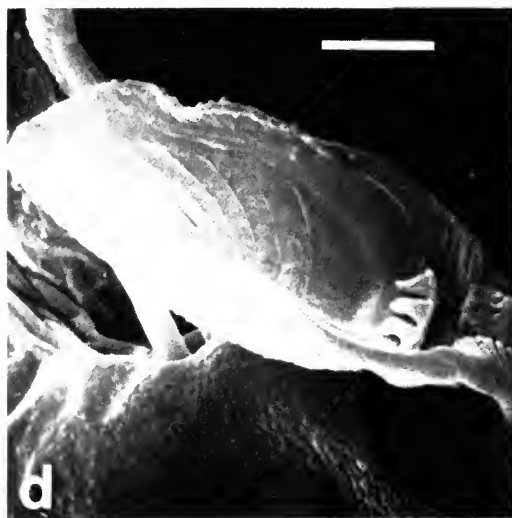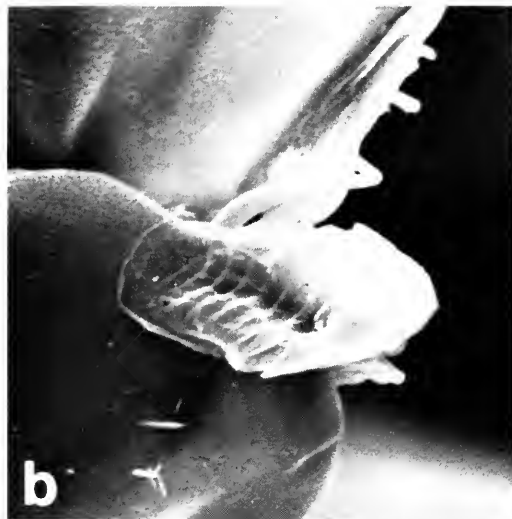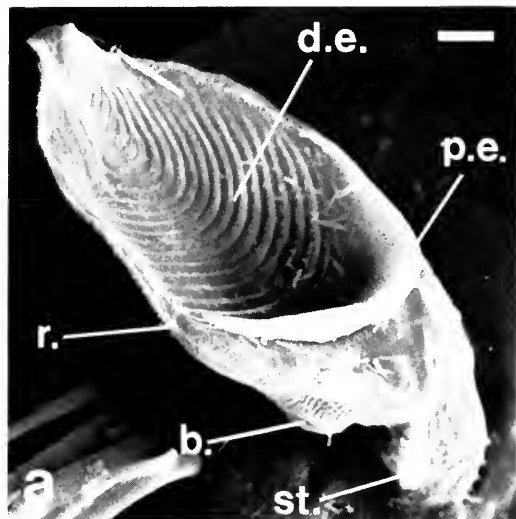
Fig. 1 a, *Gammarus pulex*, d.e., distal element; p.e., proximal element; r., receptacle; b., bulla; st., stalk: b, *Micruropus wahli*: c, *Eulimnogammarus verrucosus*: d, *Bathyporeia sarsi*: e, *Oediceroides lahillei*: f, *Parawaldeckia thomsoni*. Bar scales = 10 μm.

from 7 bands in *Bathyporeia sarsi* to about 25 in *Zaramilla kergueleni*. In both *Zaramilla* and *Bathyporeia* species the calceoli are present on the flagellum of antenna 1 and antenna 2 in the male only, and there is only one calceolus on any one flagellar article.

3. Lysianassid (Figs 1f, 2a–f)
    Amaryllus macrophthalma Haswell
    Cheirimedon similis Thurston
    Hippomedon denticulatus (Bate)
    Hippomedon holbolli (Kröyer)
    Lepidepecreum cingulatum Barnard
    Orchomene plebs (Hurley)
    Parawaldeckia thomsoni (Stebbing)
    Pseudorchomene coatsi (Chilton)
    Socarnes vahli (Kröyer)
    Tryphosella kergueleni (Miers)
    Uristes gigas Dana
    Waldeckia obesa (Chevreux)

The two surface elements of the lysianassid calceolus are more or less flattened and partially overlap, the distal element uppermost. The proximal element ranges in shape from a small crescent in *Hippomedon holbolli* to an almost circular disc in *Waldeckia obesa, Parawaldeckia thomsoni* and *Cheirimedon similis*. The distal element has weak surface banding which radiates sublongitudinally from a point close to the proximal margin in *Waldeckia, Orchomene, Parawaldeckia, Pseudorchomene, Lepidepecreum* and *Amaryllus*. In *Hippomedon, Tryphosa* and *Socarnes,* it appears quite smooth. The proximal element is only weakly concave with a slightly raised outer margin. The distal element is typically flattened, and is rather membraneous at the distal free margin. In lateral view, both surface elements rest rather freely on the receptacle with a small area of attachment near the centre. To support both surface elements the receptacle is elongated and extends almost to the distal margin of the distal element. The bulla is always well developed in the lysianassid calceolus.

One surprising and rather anomalous exception to the typical lysianassid design is found in *Uristes gigas* (Fig. 2f) which has the distal element of the calceolus strongly banded in concentric ridges that have their centre of origin close to the distal margin. This configuration has some resemblance to the pontogeneiid-type described below.

4. Pontogeneiid (Fig. 3a–d)
    Apherusa jurinei (Milne-Edwards)
    Bovallia gigantea Pfeffer
    Calliopius laeviusculus (Kröyer)
    Eusiroides monoculoides (Haswell)
    Eusiropsis riisei Stebbing
    Eusiroides stenopleura Barnard
    Halirages fulvocinctus (Sars)
    Halirages mixtus Stephensen
    Paracalliope fluviatilis (Thomson)
    Paramoera gregaria (Pfeffer)
    Pontogeneia sp.

The pontogeneiid calceolus is constructed along similar lines to the lysianassid-type, but is typically more robust with a distinctly concave proximal element and a large strongly banded distal element. The proximal element has the shape of an almost complete cup in *Bovallia gigantea* and the 5 species of *Eusiroides Eusiropsis* and *Halirages,* and is larger than the distal element in *E. monoculoides,* subequal in *E. stenopleura,* and smaller in *E. riisei.* In contrast, a relatively small crescent-shaped proximal element is found in *Calliopius laeviusculus, Apherusa jurinei* and *Paramoera gregaria,* partially overlapped by the larger
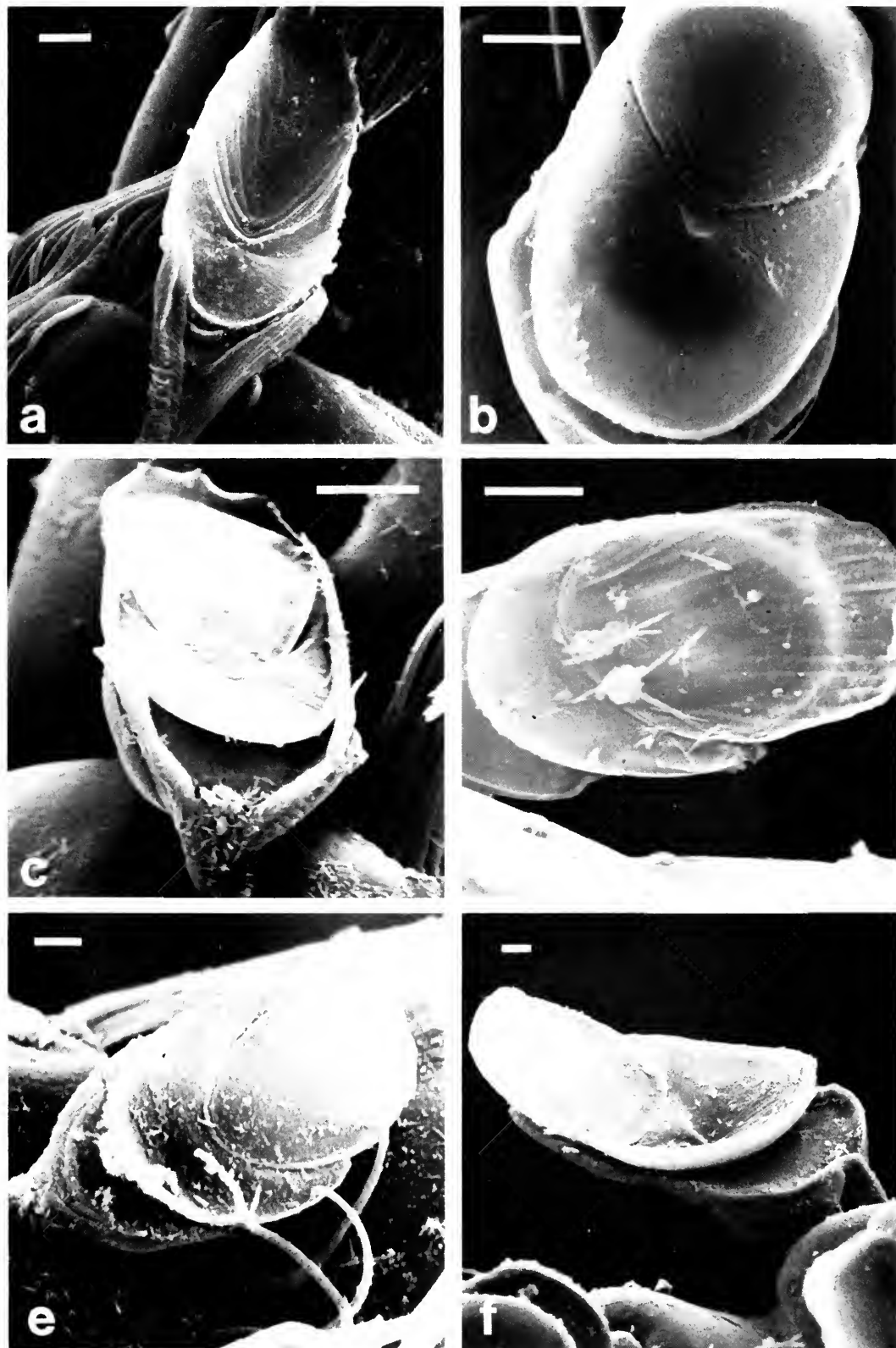
Fig. 2 a, *Orchomene plebs;* b, *Waldeckia obesa;* c, *Pseudorchomene coatsi;* d, *Hippomedon holbolli;* e, *Socarnes vahli;* f, *Uristes gigas.* Bar scales a–e = 10 µm, f = 20 µm.
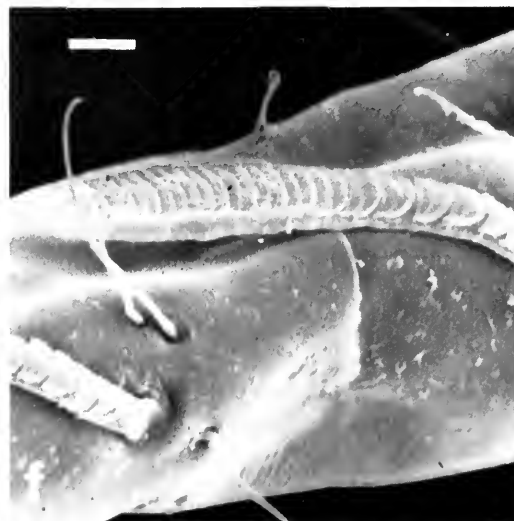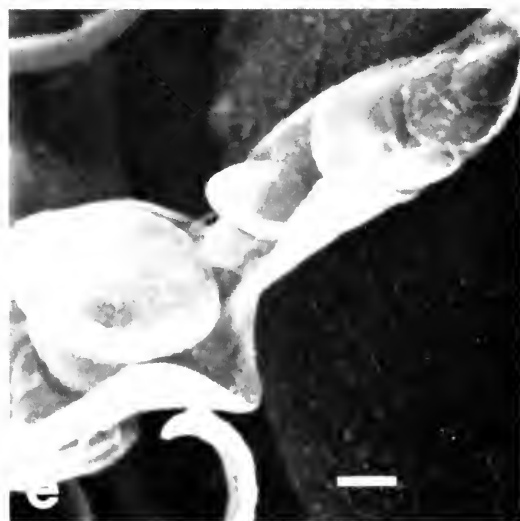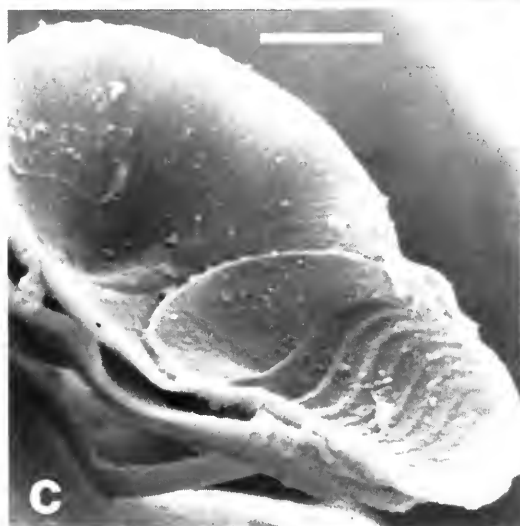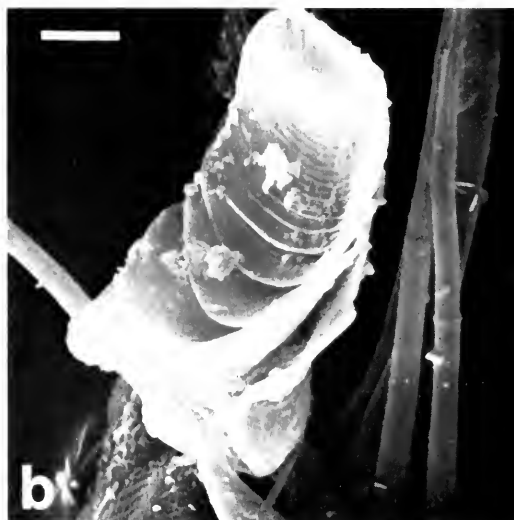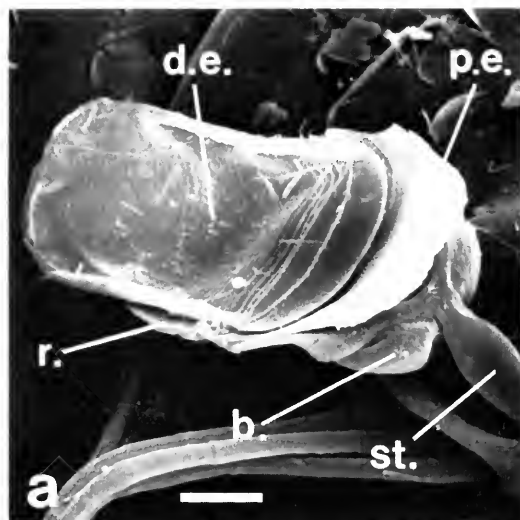
Fig. 3 a, *Calliopius laeviusculus*; d.e., distal element; p.e., proximal element; r., receptacle; b., bulla; st., stalk; b, *Paramoera gregaria*; c, *Eusiroides stenopleura*; d, *Apherusa jurinei*; e, *Chosroes incisus*; f, *Crangonyx pseudogracilis*. Bar scales a–d, f = 10 μm, e = 2 μm.

distal element. The banding of the pontogeneiid calceolus is usually transverse, sometimes weakly curved around a distal centre. Attachment of the surface elements to the elongate receptacle is like that in the lysianassid calceolus, and the bulla is similarly well developed.

5. Eusirid (Fig. 4a–d)
    Eusirus antarcticus Thomson
    Eusirus microps Walker
    Eusirus perdentatus Chevreux
    Rhachotropis aculeatus (Lepechin)
    Rhachotropis helleri (Boeck)
    Rhachotropis macropus Sars
    Schraderia gracilis Pfeffer
    Amathillopsis australis Stebbing

The special feature shared by the eusirid, gammarellid and oedicerotid types that immediately distinguishes them from other calceoli is the distinct separation of the proximal and distal elements and the remarkable cup-shaped configuration of the former. The proximal cup is robust, deeply concave, often set well apart from the distal element, and is attached to the receptacle only by a small basal connection. The following approximate measurements were obtained for the diameter of the proximal cup: *Eusirus antarcticus* 20–25 μm, *E. microps* 23–25 μm, *E. perdentatus* 25–60 μm, *Rhachotropis aculeatus* 45–70 μm, *R. helleri* 23–27 μm, *R. macropus* 23–30 μm, *Schraderia gracilis* 70 μm, *Amathillopsis australis* 25–40 μm. The distal element is elongated and carries a series of discrete crescentic plates, ranging from as few as 4 in *Rhachotropis* species and *Amathillopsis australis*, to 15 in *Eusirus antarcticus*, 25 in *Eusirus microps*, and more than 100 in *Eusirus perdentatus*. The multiplate distal element of the *Eusirus* species gives rise to an extremely elongate calceolus. The bulla at the base of the receptacle is pronounced in all eusirid calceoli.

Of all species studied the greatest development of the 'parabolic' proximal dish belongs to *Amathillopsis australis*. The largest calceolus was that sported by *Eusirus perdentatus*. The 'pore' in the apex of the distal element reported by Dahl (1975) for *Rhachotropis macropus* is not a true feature, but is an artefact produced by the rolling-up of the distal plate, probably the result of prolonged exposure to the electron beam or an excessive current.

We have included *Schraderia gracilis* in this group since it has a calceolus with an essentially eusird-type design, although the structure of the surface elements is unusual. The proximal cup in particular is enormously enlarged and saucer-shaped extending well outside the supporting receptacle, and unlike those in other eusirids appears flexible with a frayed edge to its outer margin (The somewhat collapsed state of the proximal element may be an artefact of the s.e.m. preparation).

6. Gammarellid (Fig. 3e)
    Gammarellus angulosus (Rathke)
    Gammarellus homari (Fabricius)
    Chosroes incisus Stebbing

The calceoli of these three species differ from the eusirid-type in the presence of a second cup-shaped element between the basic proximal and distal elements. Apart from this additional cup, the resemblance to the calceolus of *Rhachotropis* is quite strong. The proximal cup has a diameter of only about 8 μm in *Chosroes incisus* and 7 μm in *Gammarellus angulosus*, the intermediate cup measuring about 4·5 μm and 3·0 μm respectively.

Gammarellus and *Chosroes* are further united by the particular arrangement of the calceoli on the articles of the antennae. In both genera, the calceoli are situated in rows that extend all around the distal margins of the articles, unlike all other species examined in which calceoli are restricted to just one surface of the antenna. With the exception of *Urothoe,* the gammarellid calceoli were the smallest calceoli examined during this study.
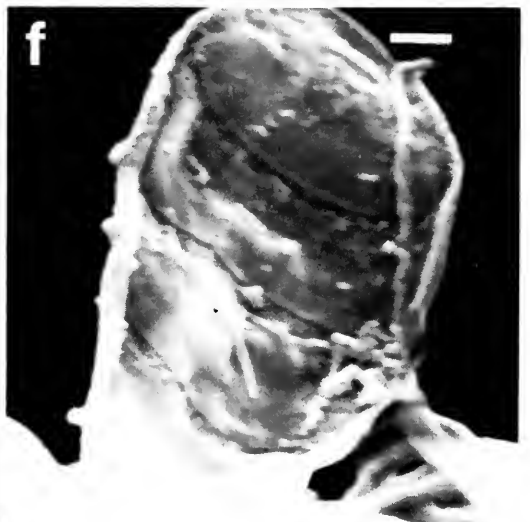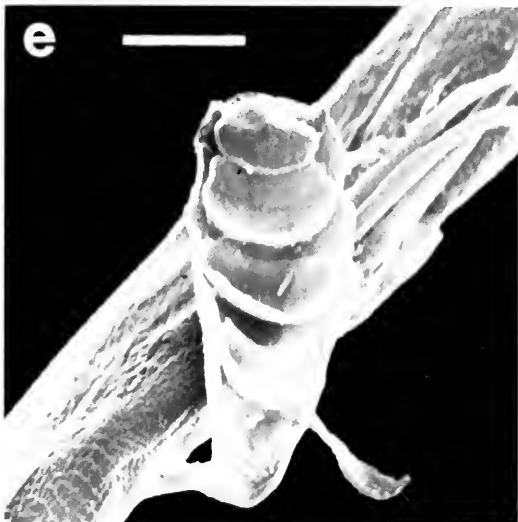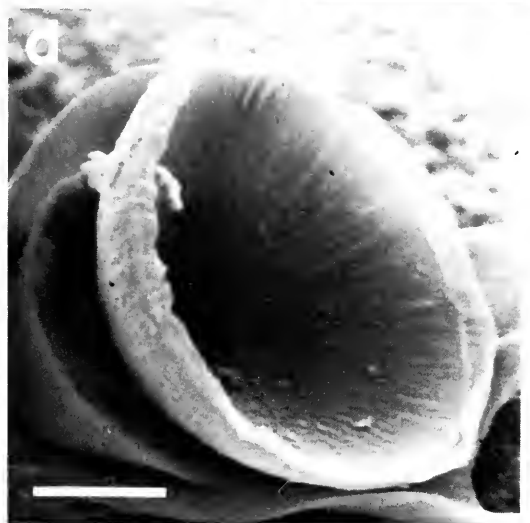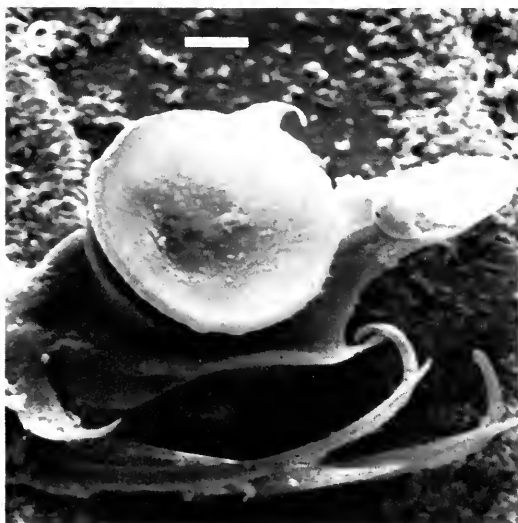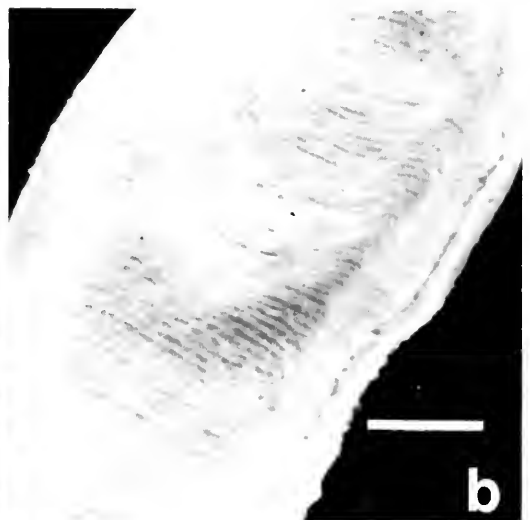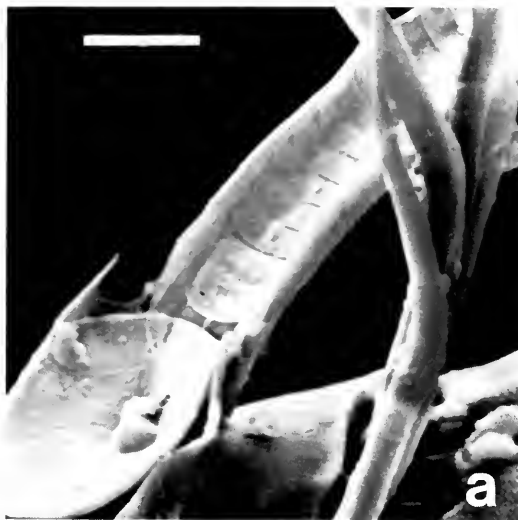
Fig. 4 a. *Eusirus antarcticus*; b, *Eusirus perdentatus*, mid part of distal element; c, *Amathillopsis australis*; d, *Amathillopsis australis*, proximal element; e, *Phoxocephalus regium*; f, *Urothoe elegans*. Bar scales a–e = 10 μm, f = 2 μm.

7. Oedicerotid (Fig. 1e)
     Oediceroides calmani Walker
     Oediceroides lahillei Chevreux
     Oediceropsis brevicornis Liljeborg

A discrete proximal cup embraced by a broad lamellar receptacle, a small suboval distal element, and a waisted receptacle characterise the oedicerotid calceolus. The distal element, which has the distal half marked with distinct transverse ridges, is attached to the spatulate extension of the receptacle at the point of the slight surface depression. The bulla at the base of the receptacle is well developed. The proximal cup has a diameter of about 25–30 μm in *Oediceroides lahillei*.

8. Phoxocephalid (Fig. 4e, f)
     Metaphoxus fultoni (Scott)
     Metaphoxus pectinatus Walker
     Paraphoxus rostratus (Dana)
     Phoxocephalus regium Barnard
     Urothoe elegans Bate

The phoxocephalid and crangonyctid calceoli differ in a number of ways from those already described although either could be derived from preceding types by a reduction in complexity.

In the phoxocephalid, the slender stalk and bulbous receptacle are absent and the surface elements are supported on a simple paddle-shaped lobe. No differentiated proximal element is apparent; instead the receptacle carries 3 to 6 oval, weakly concave plates which are probably homologous with the distal element of other calceoli. *Pontharpinia rostrata* has only 3 such plates of which the basal plate is much the largest and may represent the missing proximal element. There are 4 plates in *Phoxocephalus regium*, and 6 in *Metaphoxus pectinatus, M. fultoni,* and *Urothoe elegans.*

9. Crangonyctid (Fig. 3f)
     Crangonyx pseudogracilis Bousfield
     Synurella sp.

The crangonyctid calceolus is a greatly extended version of the phoxocephalid design. Once again there is no discrete stalk or bulbous receptacle, but a paddle-shaped lobe supporting a series of narrow plates. The plates are crescent-shaped and separated one from another proximally, but become more closely packed and much narrower distally. There are about 20 plates in *Synurella* sp. and 35 in *Crangonyx pseudogracilis.*

We interpret the series of plates as the equivalent of the distal element of other calceoli, although the generally simplistic design of both the crangonyctid and phoxocephalid-types could indicate separate evolutionary development or developments.

Discussion

(a) Calceoli function

Although various suggestions have been made as to the function of calceoli the only direct experimental work of any importance is that of Dahl and colleagues in a series of controlled aquarium experiments devised to investigate the occurrence of pheromones in amphipods (Dahl *et al.,* 1970; Dahl, 1970, 1975). Adult females of *Gammarus duebeni* Liljeborg were fed a radioactive diet of ^{3}H labelled fish liver, and were introduced into an aquarium containing unlabelled male amphipods. The two sexes were kept apart by a fine nylon-mesh partition. After 30 and 60 minutes the amphipods were isolated and specimens selected for scintillation counting and microscope autoradiography. The males had by then become radioactive, and the ^{3}H label was localized on the second antenna, either within or very close to the calceoli. Dahl and colleagues concluded that a labelled pheromone produced by the female was dispersed in the aquarium water and taken up selectively either by the male

calceoli or by the tissue in the immediate vicinity of the calceoli. (The limited resolution of the microscope autoradiographic technique used did not permit precise localization of the uptake site). In *Gammarus duebeni* only males have calceoli.

It is our belief that the labelled pheromone may have been taken up by accompanying setae seen in Dahl's figures alongside the calceoli, perhaps indicated by the presence of two uptake sites in the same transverse section (Dahl *et al.,* 1970 Fig. 3A). The solitary nature of the calceoli in *duebeni* (Fig. 1a, b) would seem to preclude the presence of two calceoli in a single transverse or obliquely transverse section. Alternatively, the calceoli may secondarily provide an avenue for pheromone uptake that is incidental to their main function. We believe that they are structurally too complex for chemoreception to be their primary role. We note that chemoreceptors in Crustacea are typically simple sac-like structures (e.g. aesthetascs), or hair-like, or funnel-canals or pores (Barber, 1961), pegs or pits. The model of a protein sieve envisaged as the basis of an aquatic chemoreceptor does not demand the range of architectural novelty characteristic of calceoli. Calceoli have a morphological complexity greater than any other aquatic receptor of equivalent size that we have encountered in the literature.

The occurrence of calceoli on males and not on females is a common feature which suggests that calceoli have some involvement in the amphipod's reproductive behaviour. Calceoli are not always confined to one sex (Hurley, 1980) but when they are it is always the male that is calceoliferous. This is consistent with Dahl's pheromone theory, but since the vast majority of amphipod species are non-calceoliferous one would have to postulate that in these pheromone receptivity had been taken over by some other receptor, or that pheromones were not part of the behavioural strategy. We had hoped that a survey of the ecological and behavioural features of calceoliferous versus non-calceoliferous species would provide a clue to function but this was not the case. Calceoliferous species are found throughout almost the full spectrum of habitats characteristic of their family groups, and from what little is known about behaviour, calceoli can be present and absent in closely allied species apparently having similar habits and modes of life.

Other arguments against chemosensitivity as a primary role—admittedly based on comparative external arrangement only—are the orientation and directionality of calceoli. Calceoli are always arranged in one or more well defined rows along the axis of the antenna, normally the underside of antenna 1 and the upper surface of antenna 2. This arrangement permits a forwardly-directed 'array' of calceoli in an animal with antenna 1 raised and antenna 2 in a lowered posture. In addition, they are clearly organised to point in the same direction relative to the antennal axis. In some species, for example *Eusirus perdentatus* and *Amathillopsis australis,* although there is only one calceolus per segment they are ranged in repetitive pairs or triplets each slightly offset from its neighbour.

Directionality is a property of the calceolus itself and is most obvious in the 'parabolic' cup reminiscent of a radar reflector found in the most specialised forms. Searching for an explanation that is compatible with complexity, orientation and directionality we are drawn to one satisfying possibility—a sensitivity to water borne pressure waves whether produced by sound waves, animal vibrations or other disturbances in the water.

One could envisage the advantages of disturbance sensors in identifying the presence or approach of other animals, whether of the same species or not, in identifying movement-disturbances or behavioural characteristics of prey, or of water disturbances in streams around stones and ripples which would enable them to seek or avoid particular ecological situations. This sonar or phono-receptor theory is not supported by experimental evidence but we are hopeful that the photographs and discussion in this paper will attract the attention of biologists and in particular electrophysiologists with the experimental facilities to probe this possibility.

(b) Phylogenetic considerations

Despite the embryonic state of knowledge about phylogenetic relationships of higher gammaridean taxa it is noteworthy that the calceoliferous families have generally been

recognised as having some evolutionary affinity (Barnard, 1969; Bousfield, 1978). Notwithstanding the passing doubts occasioned by the structure of calceoli in Phoxocephaloidea and Crangonyctoidea it seems probable that calceoli have arisen only once in the Gammaridea and have undergone limited structural radiation during the evolution of the group. In the absence of evidence pointing to convergence, similarity of calceolus design may be taken as an indicator of geneological affinity.

The discovery of close structural similarities between the calceoli of many species traditionally placed in the same genus or family and discontinuities between species from different groups, has given us confidence that calceolus architecture has phylogenetic significance. Most of the species examined and allocated to the 9 calceolus-types are in good agreement with established family groupings but there are anomalies that suggest incorrect classification. Some of the species or genera which we considered wrongly designated during the early part of our study have since been relocated in a manner consistent with the calceoli evidence (Bousfield, 1978). The important anomalies are discussed below.

Amongst the first amphipods studied were species of *Bathyporeia* and *Urothoe*, two genera that for a long time have been placed together in the Haustoriidae. The calceoli are quite different, however, pointing to separate relationships, and it was further discovered that *Urothoe* shares the calceolus type of *Phoxocephalus*. This supports fully the recent revision by Bousfield (1978) in which *Urothoe* is moved from the haustoriids to a new family alongside *Phoxocephalus* in the superfamily Phoxocephaloidea. The bathyporeid-type calceolus is shared by *Zaramilla,* a genus placed in the Eusiridae by Barnard (1969), although special reference was made to its apparent 'haustoriid' affinities. There can be little doubt that *Zaramilla* belongs close to *Bathyporeia,* and the marked similarity of their calceoli to the gammarid-type (especially *Anisogammarus confervicolous*) must be further evidence for the proximity of the Pontoporeiidae to the gammaroid families.

Calceoli may prove particularly useful in re-assessing the Eusiridae, a family recently made very large and unwieldly by the inclusion of the families Pontogeneiidae and Calliopiidae (Barnard, 1969, 1972). Eusirid amphipods are frequently calceoliferous and have some of the largest and structurally most complex calceoli known. We have recognised 3 types within the eusirid complex—pontogeneiid, eusirid and gammarellid—and our allocation of species to each of these tends to cut across previously accepted family boundaries. Thus, the 'calliopiids' *Calliopius, Apherusa, Halirages* and *Paracalliope* share the same type of calceolus as the 'pontogeneiid' *Pontogeneia,* and the 'eusirids' *Eusiroides, Eusiropsis, Bovallia* and *Paramoera. Eusirus* and *Rhachotropis,* traditionally confamilial, must be joined by *Amathillopsis,* a genus having a chequered history being variously allocated to the Gammaridae, Amathillopsidae and the Paramphithoidae. We have placed *Schraderia* with our eusirids since it shares the same basic calceolus design, although it differs somewhat in detail and relative proportions.

The third group mentioned in the eusirid context, the gammarellid-type, brings together *Gammarellus* and *Chosroes,* linked by the common possession of an intermediate cup-shaped surface element. *Gammarellus* was, until its transfer to a new family (Bousfield, 1977) assigned to the Gammaridae, and *Chosroes* was with the calliopiids. If Bousfield's new family Gammarellidae receives general acceptance by amphipodologists, then *Chosroes* must be considered for inclusion also. It is particularly satisfying to note that, as well as having similar calceoli, *Gammarellus* and *Chosroes* (figured Sars, 1894; Stebbing, 1888) show a surprising similarity in many characters.

New perspectives produced by this SEM study should encourage other taxonomists to pay greater attention to this microscopic antennal receptor so often ignored in systematic descriptions, and, we hope, encourage some physiological work on their structure and function.

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A new species of *Lernaea* (Copepoda: Cyclopoida) from Papua—New Guinea

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Introduction

In his recent synopsis of the genus *Lernaea* Linn., 1758 Kabata (1979) recognized 37 species. All of these parasitise freshwater fishes although some are also known to occur on amphibian tadpoles. Eleven species have been reported from India, S.E. Asia and the Far East (Kabata, 1979) but no records of *Lernaea* from the Australasian zoogeographic region have as yet been published. In October 1979 some *Lernaea* were collected by Dr I. L. Owen of the Central Veterinary Laboratory, Port Moresby, Papua-New Guinea. The specimens were found to represent a new species which is described in detail below. Specimens were examined and dissected in lactophenol. Drawings were made using a camera lucida and terminology is adapted from Kabata (1979).

Description of new species

Lernaea papuensis n. sp.

Postmetamorphosis adult female (Fig. 1A); cephalothorax small, hemispherical, bearing antennae and mouthparts ventrally and with nauplius eye visible through integument dorsally (Fig. 1B). Holdfast apparently comprising 6 subequal arms, probably representing an unbranched dorsal pair and a ventral pair, with each member being divided at its origin into 2 equal branches. Holdfast usually arranged in anteroposterior plane, sometimes dorsal pair pass perpendicularly into dorsoventral plane (Fig. 2D). Holdfast arms of largest paratype (Fig. 2E) distorted and overlapping due to site on host. Neck, comprising second to fourth leg-bearing somites, passing imperceptibly into genital somite. Neck expanding in girth posteriorly but marked with conspicuous swellings, each delimited by constrictions, anterior to legs 2 and 3. Genital somite with simple hemispherical genital prominence posteriorly. Abdomen conical, unsegmented and bearing uropods distally. Total body length from anteriormost tip of holdfast to posterior tip of uropod ranging from 5·4 to 10 mm.

First antenna (Fig. 1C) indistinctly 4-segmented; segments 1 to 4 bearing 10, 3, 4, and 10 armature elements respectively. Second antenna (Fig. 1D) indistinctly 3-segmented, segments 1 and 2 unarmed and comprising half total length of appendage, segment 3 with 3 setae on posterior margin, and a claw-like spine, 5 slender setae and 1 setule distally. Labrum (Fig. 1B) a flattened triangular plate, overlying mandibles and first maxillae. Second maxilla (Fig. 1E) 2-segmented with 2 curved claws apically. Maxilliped (Fig. 1F) basal segment with small papilla, armed with an apical setule, on distal part of medial margin; terminal segment with 5 strong curved spines apically.

Thoracic legs 1 to 4 more or less regularly spaced along body; leg 1 situated on ventral surface of cephalothorax at posterior border of cephalothorax (Fig. 1A 1), legs 2 to 4 (Fig. 1A 2–4) on ventral surface of neck. Legs biramous with 3-segmented rami (Figs 1G, 2A–C), armature formula as follows:

Bull. Br. Mus. nat. Hist. (Zool.) **40** (4) : 117–120

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Fig. 1 *Lernaea papuensis* n. sp. female. A, Holotype, dorsal; B, paratype head and cephalic appendages, ventral; C, first antenna, ventral; D, second antenna, ventral; E, second maxilla, posteroventral; F, maxilliped, posteroventral; G, first leg, anterior; H, uropods, dorsal. Scales 50 μm unless otherwise stated.

	coxa	basis	endopod	exopod
Leg 1	0–1	1–I	0–1;0–1;4,II	I–1;I–1;II,5
Leg 2	0–1	1–0	0–1;0–2;4,II	I–1;I–1;III,5
Leg 3	0–1	1–0	0–1;0–2;4,II	I–1;I–1;III,5
Leg 4	0–1	1–0	0–1;0–2;3,II	I–1;I–1;III,5

Several long pinnules present near mediodistal angle of basis of legs 2 to 4. Lateral margins of all endopod segments armed with pinnules. Leg 5 not observed.

Uropods (Fig. 1H) subcylindrical, about 1·5 times longer than wide and bearing a very long plumose seta on distal margin, a short lateral seta, dorsal seta and posterolateral seta.
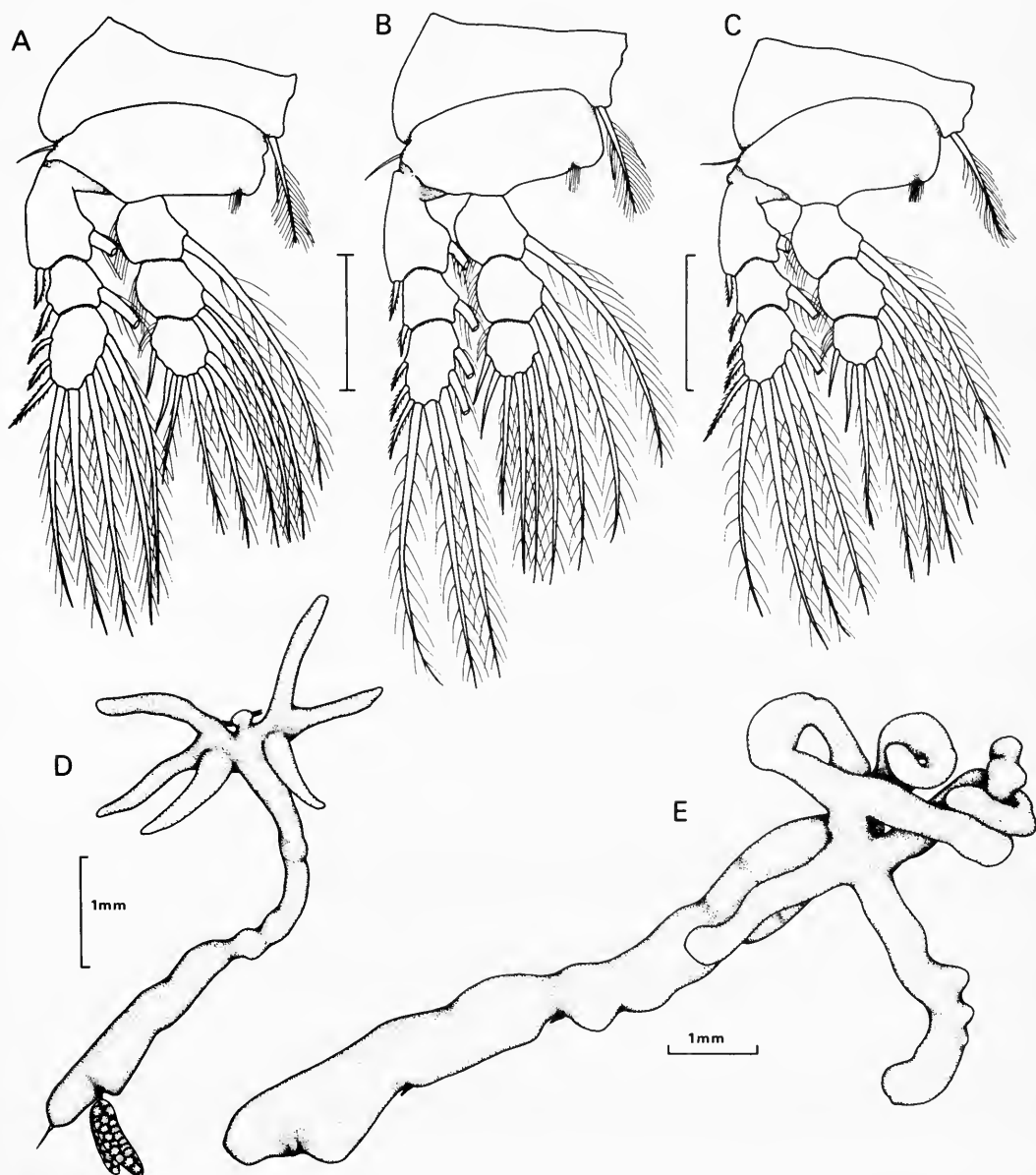
Fig. 2 *Lernaea papuensis* n. sp. paratype female. A, second leg, posterior; B, third leg, posterior; C, fourth leg, posterior; D, smallest ovigerous paratype, dorsal; E, largest paratype, dorsal. Scales 50 μm unless otherwise stated.

MATERIAL EXAMINED. Holotype ♀, 9 paratype ♀♀ from gill arches, pectoral fins and body surface of Jardine's Barramundi, *Scleropages jardini* Kent, caught in the Bensbach river, Western Province, Papua–New Guinea. BM(NH) Reg. Nos holotype 1980. 122, paratypes 1980. 123–131.

REMARKS. Although the size and shape of the holdfast of *Lernaea* species is variable with age and especially with position on the host (Fryer, 1961) it is the gross morphology of the holdfast and trunk which provides virtually all the characters used to distinguish between the species (Harding, 1950). This situation arises because of the high degree of uniformity of appendage structure and armature throughout the genus (Harding, 1950; Kabata, 1979).

The new species differs from all others in the possession of a holdfast comprising 6 slender, elongate arms which are more or less equal in length. The holdfast of *L. papuensis* could be derived from the condition exhibited by *L. senegali* Zimmermann, 1923 which possesses a pair of simple dorsal arms and a pair of ventral arms which are branched near their tips. The 4 ventral arms of the holdfast of *L. papuensis* are probably homologous with the branched ventral pair of *L. senegali* but they are branched at their bases. The genital prominence is hemispherical in both the new species and *L. senegali.* Another important taxonomic character of *L. papuensis* is the shape of the neck. The conspicuous expansions of the neck, delimited by constrictions, anterior to leg 2 and particularly to leg 3, are more marked in this species than in the majority of *Lernaea* species.

Acknowledgements

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Some type specimens of Isopoda (*Flabellifera*) in the British Museum (Natural History), and the isopods in the Linnaean Collection

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Introduction

British Museum (Natural History) collection

The first catalogue of the crustacean collection was compiled by Adam White and published in 1847. The foundation of that collection was W. E. Leach's material, acquired by the Museum in 1826. This contained the type material of approximately 140 crustacean species described by Leach, 37 of which belong to the suborder Flabellifera. Between 1826 and the publication of White's catalogue the collection was augmented from various sources. The most notable additions to the marine Isopoda were from the collections of George Montagu, Thomas Say, and those made during the voyages of H. M. Ships *Erebus* and *Terror* to the Antarctic.

In 1863 the Museum acquired from the Linnean Society Sir Joseph Banks' collection. Unlike the insects, the crustaceans from Banks' collection were not registered, and no record exists of the species it contained. Five species of *'Oniscus'* described by J. C. Fabricius (1775) were from Banks' collection, and although the types of all five were considered by Zimsen (1964) to be lost, recent investigations have established that two of these, *Ceratothoa imbricata* and *Serolis paradoxa* are still in the BM(NH) collections*. The other three species are amphipods (see Stebbing, 1888).

In the latter half of the nineteenth century the dry collection of isopods was augmented from various sources, especially from the voyages of H. M. Ships *Herald* and *Rattlesnake* (see Miers, 1884 p. 179). It also included the type material of several species described by E. J. Miers, the Assistant in charge of Crustacea from 1872 to 1885 (see Gordon, 1971).

Although parts of the Crustacea collection have been catalogued since 1847 (see Bell, 1855; Bate, 1862; Thurston & Allen, 1969; Lincoln & Ellis, 1974; Lincoln & Hurley, 1974; Ellis & Lincoln, 1975), this is the first attempt since White's to catalogue the marine isopods, and this paper is intended as a precursor to a catalogue of the entire flabelliferan type collection which contains an estimated 200 species from some 50 genera.

The Linnaean collection

Linnaeus' collection was bought from his widow by J. E. Smith in 1774. It remained in Smith's possession until his death in 1828, and a year later it was purchased by the Linnean Society of London.

The isopod collection, preserved dry, now consists of 13 specimens (see p. 127) labelled in Linnaeus' handwriting and which must be considered holotypes. (A specimen labelled '*ceti*' included among these is the parasitic amphipod *Cyamus ceti* (L., 1758).) There are also 28

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*The holotypes of *Serolis paradoxa* and *Ceratothoa imbricata* were collected during Capt. Cook's first voyage (1768–1771). Much of the zoological material collected during Cook's voyages has become widely dispersed and/or lost, and these specimens were overlooked when Whitehead (1969) compiled his account of the traceable specimens.

unlabelled specimens that have been provisionally determined. These comprise: 4 *Exosphaeroma gigas* (Leach, 1818); 2 *Exosphaeroma* sp.; 4 *Parisocladus perforatus* (Edwards, 1840); 1 *Idotea carinata,* Miers 1881 (= *Synisoma* sp.); 1 *Paridotea ungulata* (Pallas, 1772); 1 *Paridotea rubra* Barnard, 1914; 1 *Aega tridens* Leach, 1815; 2 *Ceratothoa imbricata* (Fabricius, 1775); 1 amphipod (family Stegocephalidae); 1 *Ligidium* sp.; 1 *Asellus aquaticus* (L., 1758) (anterior half only); 1 *Nerocila serra* Schiodte & Meinert, 1881; 1 *Idotea granulosa* Rathke, 1843; 1 *Idotea chelipes* (Pallas, 1766); 1 *Ligia dilatata* Brandt, 1833; 1 *Ligia oceanica* (L., 1767); 4 Oniscoidea.

Smith was known to have augmented Linnaeus' zoological collection with material of his own (Jackson, 1890) and these unlabelled specimens may have been added by him.

Methods

Until the latter half of the nineteenth century, small crustaceans were curated at the BM(NH) in a similar manner to entomological specimens *i.e.* impaled with entomological pins and stored dry in insect cabinets. Throughout the last 150 years the condition of many of these crustaceans has deteriorated, chiefly resulting from repeated movement of the dry collection. Appendages have become detached, specimens broken in half, and a few have disintegrated completely. To prevent further deterioration of valuable type material and to make it more easily accessible for study, a decision was taken to transfer specimens to alcohol for incorporation in the Museum's spirit collection. The techniques used for rendering the dried specimens suitable for alcohol preservation are given below.

In order to allow restorative chemicals to penetrate the body tissues air must be expelled from the specimen. Sometimes this can be achieved following direct immersion into 80% IMS (industrial methylated spirit). If the specimen fails to sink gentle heat should be applied until the solution reaches boiling point, immediately after which the container should be allowed to cool. Following either procedure the air-free specimen is placed into distilled water for one hour and then relaxed using one of the chemical methods described below, each of which has particular advantages or disadvantages as noted. After this chemical treatment the specimen is again immersed into distilled water for one hour and then transferred to 80% IMS for storage.

Chemical treatments

All solutions were made with distilled water.

(*a*) 1·2% sodium chloride. Length of time: dependent on size of specimen, 4–5 hours for small specimens; up to 24 hours for large specimens. This method takes longer than others, but this can be an advantage with small or fragile specimens.

(*b*) 2% tri-sodium orthophosphate. Length of time: 4–6 hours. A close watch must be kept on the specimens from 4 hours onwards, as they may become too flaccid. A further disadvantage of this technique is that a cloying, flocculent precipitate may develop, mostly at the bases of the appendages. As this precipitate has to be removed by mechanical means, damage to the specimen can occur unless extreme care is taken.

(*c*) 0·5% formaldehyde OR 5% sodium sulphate. Length of time: $3\frac{1}{2}$–6 hours, but may safely be left overnight as prolonged immersion does not seem to be deleterious.

(*d*) 2% citric acid and 20% sodium citrate in equal parts. Length of time: up to 4 hours. In the limited trials of this technique, the specimens have a tendency to become too flaccid.

(*e*) Sandison's technique: 90% ethyl alcohol—30 volumes; 0·5% formaldehyde—50 volumes; 5% sodium citrate—20 volumes. Length of time: 1–24 hours. The results produced by this technique were very variable. Reasonable results were obtained when fragile specimens were immersed for 1–2 hours, but larger, more robust specimens sometimes remained largely unaffected.

British Museum (Natural History) Collection

AEGIDAE

Aega bicarinata Leach (1818 : 349)
 HOLOTYPE: 1979 : 306 : 1. Mediterranean? Presented by W. E. Leach.
Aega emarginata Leach (1815 : 370) [transferred to *Aega psora* (L., 1758)]
 HOLOTYPE: 1979 : 309 : 1. Locality unknown. Presented by W. E. Leach.
Aega meinerti Miers (1884 : 305)
 HOLOTYPE: 1858 : 172. King George Sound, Western Australia. Presented by F. M. Rayner, H.M.S. *Herald.*
Aega monophthalma Johnston (1834 : 233)
 HOLOTYPE: 1979 : 299 : 1. Berwick Bay, Northumberland. On large codfish. Presented by G. Johnston.
Rocinela danmoniensis Leach (1818 : 349)
 HOLOTYPE: 1979 : 328 : 1. Plymouth Sound. Presented by W. E. Leach.

CIROLANIDAE

Cirolana cranchi Leach (1818 : 347)
 HOLOTYPE: 1979 : 279 : 1. Falmouth, Cornwall. Presented by Mr Cranch.
Cirolana harfordi (Lockington) (1877 : 46, as *Aega harfordi*)
 PARATYPES: 1878 : 9 (4 specimens). Santa Rosa Island. Under stones, MT, in muddy places. Collected by W. G. W. Harford. Presented by W. N. Lockington & W. G. W. Harford.
Cirolana rossi Miers (1876a : 228)
 SYNTYPES. 1856 : 33 (2 specimens). New Zealand. H.M.S. *Herald.* Purchased of Mr *Erebus*—The Antarctic Voyage'. Presented by Lieut. A. Smith.
 SYNTYPES: 1844 : 3 (7 specimens). Auckland Is. Antarctic Expedition. Presented by Capt. James Clarke Ross.
 SYNTYPE: 1848 : 80. New Zealand. Collected by Rev. W. Colenso. Presented by Dr J. Hooker.
 SYNTYPE: 1856 : 33 (2 specimens). New Zealand. H.M.S. *Herald.* Purchased of Mr Cuming.
Cirolana tenuistylis Miers (1884 : 303)
 SYNTYPES: 1862 : 53 (2 specimens). Locality unknown. Collected by F. M. Rayner, H.M.S. *Herald.* Presented by Mr Warwick.
Conilera montagui Leach (1818 : 348) [transferred to *Conilera cylindracea* (Montagu, 1804)]
 HOLOTYPE: 1979 : 289 : 1. Salcombe, Devonshire. Presented by G. Montagu.
Eurydice pulchra Leach (1818 : 370)
 SYNTYPES: 1979 : 290 (2 specimens). Bantham, Devonshire. Presented by W. E. Leach.
Nelocira swainsoni Leach (1818 : 347) [transferred to *Cirolana cranchi* Leach, 1818]
 SYNTYPES: 1979 : 288 (3 specimens). Sicily. Collected and presented by W. Swainson.

CYMOTHOIDAE

Anilocra capensis Leach (1818 : 350)
 SYNTYPES: 1979 : 329 (3 specimens). Cape of Good Hope. Presented by W. E. Leach.
Anilocra cuvieri Leach (1818 : 350) [transferred to *Anilocra physodes* (L., 1758)]
 SYNTYPES: 1979 : 332 (3 specimens). Island of Iviça (Ibiza?), Mediterranean. Presented by G. Cuvier.
Anilocra mediterranea Leach (1818 : 350) [transferred to *Anilocra physodes* (L., 1758)]
 HOLOTYPE: 1979 : 330 : 1. Sicily. Presented by W. E. Leach.
Canolira rissoniana Leach (1818 : 350) [= *Anilocra* sp.]
 HOLOTYPE: 1979 : 331 : 1. Locality unknown. Presented by W. E. Leach.
Ceratothoa imbricata (Fabricius) (1775 : 296, as *Oniscus*)

HOLOTYPE: 1979 : 403 : 1. New Zealand, Capt. Cook's first voyage. Sir Joseph Banks' collection. Presented by the Linnean Society of London.

Cymothoa banksii Leach (1818 : 353) [transferred to *Ceratothoa imbricata* (Fabricius, 1775)]

HOLOTYPE: 1979 : 402 : 1. New Zealand. Presented by W. E. Leach.

Cymothoa dufresni Leach (1818 : 352) [transferred to *Cymothoa oestrum* (L., 1758)]

SYNTYPES: 1979 : 405 (2 specimens). Locality unknown. Presented by W. E. Leach.

Cymothoa leschenaultii Leach (1818 : 352) [transferred to *Cymothoa eremita* (Brünnich, 1783)]

HOLOTYPE: 1979 : 406 : 1. Pondicherry, India. Presented by Leschenault.

Cymothoa mathieui Leach (1818 : 353) [transferred to *Cymothoa eremita* (Brünnich, 1783)]

SYNTYPES: 1979 : 407 (2 specimens). 'Ile-de-France'. Presented by M. Mathieu.

SYNTYPE?: 1979 : 408. 'Ile-de-France'. Sir Joseph Banks' collection. Presented by the Linnean Society of London.

Cymothoa trigonocephala Leach (1818 : 353) [transferred to *Ceratothoa imbricata* (Fabricius, 1775)]

SYNTYPES: 1979 : 404 (2 specimens). Locality unknown. Presented by W. E. Leach.

Lironeca contracta Miers (1880 : 466, footnote)

SYNTYPE: 1844 : 105. Australia. Presented by the Earl of Derby.

SYNTYPE: 1846 : 89. Australia. Presented by J. B. Jukes.

Lironeca desmarestii Leach (1818 : 352) [transferred to *Lironeca redmani* Leach, 1818]

SYNTYPES: 1979 : 336 (3 specimens). Locality unknown. Presented by W. E. Leach.

Lironeca laticauda Miers (1877 : 677)

SYNTYPES: 1862 : 96 (2 specimens). Manchuria. Purchased of Stevens.

Lironeca micronyx Miers (1880 : 466, footnote)

SYNTYPES: 1846 : 104 (3 specimens). Mauritius. Presented by R. Templeton.

Lironeca novaezealandiae Miers (1876a : 228) [transferred to *Lironeca raynaudi* Milne Edwards, 1840]

SYNTYPES: 1845 : 30 (2 specimens). New Zealand. Presented by Mr Earl.

Lironeca ovalis (Say) (1818a : 394, as *Cymothoa*)

SYNTYPE: 1979 : 413. N. America. Presented by T. Say.

Lironeca rafineskii Leach (1818 : 352)

SYNTYPES: 1979 : 338 (2 specimens). Cape of Good Hope? (but see original description—'localité inconnu'). Presented by W. E. Leach.

Lironeca redmani Leach (1818 : 352)

HOLOTYPE: 1979 : 401 : 1. Jamaica. Presented by Lieut. Redman.

Lironeca vulgaris Stimpson (1857 : 508). See also Stimpson 1859 : 88

SYNTYPES: 1878 : 9 (3 specimens). San Francisco Market. Presented by W. N. Lockington & W. G. W. Harford.

Nerocila blainvillei Leach (1818 : 351)

SYNTYPES: 1979 : 400 (2 specimens). Sicily? (but see original description—'localité inconnu'). Presented by W. E. Leach.

Nerocila congener Miers (1880 : 468, footnote)

HOLOTYPE: 1979 : 337. Philippine Islands. Presented by Mr Cuming.

Nerocila longispina Miers (1880 : 468)

HOLOTYPE: 1849 : 86. Malabar. Presented by I. Ward.

Nerocila macleayi Miers (1884 : 301) [nom. nov. for *Nerocila imbricata* (Fabricius): Miers 1876a *vide* Miers 1884]

SYNTYPE: 1845 : 30 (as *Nerocila imbricata* (Fabricius): White 1847) New Zealand. Presented by Mr Earl.

SYNTYPE: 1979 : 414 : 1 (as *Nerocila imbricata* (Fabricius): White 1847). Locality and donor unknown.

SYNTYPE: 1979 : 417 : 1 (as *Cilonera macleayii* White & Doubleday 1843 *nom. nud.*). 'Africa'. Presented by W. E. Leach.

SYNTYPE: 1842 : 44 (as *Cilonera macleayii* White & Doubleday 1843 *nom. nud.*). New Zealand. Presented by Andrew Sinclair.

SYNTYPE: 1847 : 104. New Zealand. Presented by Andrew Sinclair.

SYNTYPE: 1979 : 415 : 1. New Zealand 'taken out of the mouth of a fish'. Presented by Andrew Sinclair.

SYNTYPE: 1850 : 12. West coast, America. Presented by Capt. Kellett & Lieut. Wood.

SYNTYPE: 1979 : 416 : 1. Locality and donor unknown.

Nerocila trichiura (Miers) (1877 : 677, as *Anilocra*)

HOLOTYPE: 1846 : 104. Mauritius. Presented by Robert Templeton.

Olencira lamarckii Leach (1818 : 351) [transferred to *Olencira praegustator* (Latrobe, 1802)]

HOLOTYPE: 1979 : 333 : 1. Locality unknown. Presented by W. E. Leach.

LIMNORIIDAE

Limnoria terebrans Leach (1814 : 433) [transferred to *Limnoria lignorum* (Rathke, 1799)]

SYNTYPES: 1979 : 445 (3 specimens). Bell Rock, Scotland. Collected by R. Stevenson. Presented by W. E. Leach.

SEROLIDAE

Serolis fabricii Leach (1818 : 340) [transferred to *Serolis paradoxa* (Fabricius, 1775)]

HOLOTYPE: 1979 : 452 : 1. Senegal. Presented by W. E. Leach.

Serolis latifrons Miers (1875*a* : 74)

SYNTYPE: 1843 : 70. Rendezvous Cove, Auckland Is. 'Collected in the *Erebus*—The Antarctic Voyage'. Presented by Lieut A. Smith.

Serolis paradoxa (Fabricius) (1775 : 296, as *Oniscus*)

HOLOTYPE: 1979 : 451 : 1. Tierra del Fuego, Capt. Cook's first voyage. Sir Joseph Banks' collection. Presented by the Linnean Society of London.

Serolis septemcarinata Miers (1875*b* : 116)

SYNTYPES: 1843 : 70 (2 specimens). Crozet Islands. 'Collected in the *Erebus* during the Antarctic voyage'. Presented by Lieut. A. Smith.

SPHAEROMATIDAE

Ancinus depressus (Say) (1818*b* : 483, as *Naesa*)

SYNTYPE: 1979 : 444 : 1. North America. Presented by Thomas Say.

Campecopea cranchi Leach (1818 : 341) [transferred to *Campecopea hirsuta* (Montagu, 1804)]

SYNTYPES: 1979 : 441 (2 specimens). Falmouth, Cornwall. Collected by Mr Cranch. Presented by W. E. Leach.

Campecopea hirsuta (Montagu) (1804 : 71, as *Oniscus*)

SYNTYPES: 1979 : 440 (3 specimens). Devon. Presented by G. Montagu.

Cassidinidea ovalis (Say) (1818*b* : 484, as *Naesa*)

SYNTYPE: 1979 : 422 : 1. North America. Presented by Thomas Say.

Cilicaea antennalis Miers (1884 : 310)

HOLOTYPE: 1979 : 442 : 1. Swan River, W. Australia. Presented by Sir J. Richardson.

Cilicaea latreillei Leach (1818 : 342)

SYNTYPES: 1979 : 443 (2 specimens). Locality unknown. Presented by W. E. Leach.

Cilicaea latreillei var. *longispina* Miers (1884 : 310)

HOLOTYPE: 1851 : 33. Bass Strait. HMS *Rattlesnake*. Presented by J. Macgillivray.

Cymodoce bifida Leach (1818 : 343)

HOLOTYPE: 1979 : 431. Locality unknown. Presented by W. E. Leach.

Cymodoce convexa Miers (1876*a* : 229)

SYNTYPES: 1852 : 43 (3 specimens). New Zealand. Purchased of Mr Cuming.

Cymodoce emarginata Leach (1818 : 342)
   SYNTYPE: 1979 : 434 : 1. Mount Edgecombe, near Plymouth, Devon. Variety 'a'. Collected and presented by W. E. Leach.
   SYNTYPE: 1979 : 435 : 1. Falmouth, Cornwall. Variety 'b'. Collected by Mr Cranch. Presented by W. E. Leach.
Cymodoce lamarcki Leach (1818 : 343) [transferred to *Cymodoce truncata* Leach, 1814]
   SYNTYPES: 1979 : 436 (2 specimens). Sicily. Collected by W. Swainson. Presented by W. E. Leach.
Cymodoce truncata Leach (1814 : 433)
   HOLOTYPE: 1979 : 439 : 1. Devon. Presented by W. E. Leach.
Dynamene montagui Leach (1818 : 344) [transferred to *Dynamene bidentata* (Adams, 1800)]
   SYNTYPES: 1979 : 430 (3 specimens). Devon. Presented by G. Montagu.
Dynamene rubra Leach (1818 : 344) [transferred to *Dynamene bidentata* (Adams, 1800)]
   SYNTYPES: 1979 : 428 (4 specimens). Devon. Presented by W. E. Leach.
Dynamene viridis Leach (1818 : 344) [transferred to *Dynamene bidentata* (Adams, 1800)]
   SYNTYPES: 1979 : 429 (3 specimens). Devon. Presented by W. E. Leach.
Exosphaeroma coatsi Tattersall (1913 : 885)
   SYNTYPE: 1979 : 425 (fragment). St. Paul Island, Indian Ocean. Presented by J. Macgillivray.
Exosphaeroma gigas (Leach) (1818 : 346, as *Sphaeroma*)
   SYNTYPE: 1941 : 6 : 27 : 5. Locality unknown. Presented by W. E. Leach.
   SYNTYPE: 1979 : 420 : 1. Locality unknown. Sir Joseph Banks' collection. Presented by the Linnean Society of London.
Exosphaeroma kraussi Tattersall (1913 : 884)
   SYNTYPES: 1881 : 19 (14 specimens). Sea Point, Cape Town, South Africa. Presented by A. E. Craven.
Exosphaeroma lanceolatum (White) (1843 : 345, as *Sphaeroma gigas* var. *lanceolatum*)
   SYNTYPES: 1842 : 4 (White (1847 : 102) refers to 4 specimens, but there are 7 with this registration number). Falkland Islands. Presented by W. E. Wright.
Isocladus spiniger var. *recurvatus* Miers (1876*b* : 113) [transferred to *Isocladus armatus* (Milne Edwards, 1840)]
   HOLOTYPE: 1856 : 164. New Zealand. Presented by Dr Sinclair.
Isocladus tristensis (Leach) (1818 : 345, as *Sphaeroma*)
   SYNTYPES: 1979 : 453 (4 specimens). Tristan d'Acunha. Collected by Capt. Carmichael. Presented by W. E. Leach.
Sphaeroma curtum Leach (1818 : 345) [transferred to *Cymodoce truncata* Leach, 1814]
   HOLOTYPE: 1979 : 418 : 1. Britain. Presented by W. E. Leach.
Sphaeroma dumerilli Leach (1818 : 345) [transferred to *Cymodoce truncata* Leach, 1814]
   SYNTYPES: 1979 : 432 (2 specimens). Genoa. Presented by W. E. Leach.
   SYNTYPE: 1979 : 433. Sicily. Presented by W. E. Leach.
Sphaeroma hookeri Leach (1814 : 433)
   SYNTYPES: 1979 : 421 (4 specimens). Suffolk [Leach (1814) gives locality as Norfolk, but see Leach (1815 : 369; 1818 : 345)]. Collected by W. J. Hooker. Presented by W. E. Leach.
Sphaeroma olivacea Lockington (1877 : 45) [transferred to *Gnorimosphaeroma oregonensis* (Dana, 1853)]
   SYNTYPES: 1878 : 9 (3 specimens). San Francisco Bay. Presented by W. N. Lockington & W. G. W. Harford.
Sphaeroma prideauxianum Leach (1818 : 345) [transferred to *Cymodoce truncata* Leach, 1814]
   HOLOTYPE: 1979 : 423 : 1. Devon. Collected by C. Prideaux. Presented by W. E. Leach.
Sphaeroma quadridentatum Say (1818*a* : 400)
   SYNTYPES: 1979 : 419 (4 specimens). St Catherine Island, Georgia, U.S.A. Presented by T. Say.

Sphaeroma rugicauda Leach (1814 : 405 & 433)

SYNTYPES: 1979 : 424 (5 specimens). Ulva I., Argyll, Scotland. Presented by W. E. Leach.

Zuzara diadema Leach (1818 : 344)

HOLOTYPE: 1979 : 426 : 1 (fragment). Australia. Collected by R. Brown. Presented by W. E. Leach.

Zuzara semipunctata Leach (1818 : 344)

HOLOTYPE: 1979 : 427 : 1. Locality unknown. Presented by W. E. Leach.

Linnaean Collection

Oniscus asilus L. (1758 : 636) [redet. *Nerocila* sp.]

Cymothoa oestrum (L.) (1758 : 636)

Aega psora (L.) (1758 : 636)

Anilocra physodes (L.) (1758 : 636)

Saduria entomon (L.) (1758 : 636)

Oniscus marinus L. (1758 : 637) [= *Idotea neglecta* Sars, 1897. See Heegard & Holthuis (1960)]

Idotea linearis (L.) (1767 : 1060)

Asellus aquaticus (L.) (1758 : 637)

Ligia oceanica (L.) (1767) : 1061)

Oniscus assimilis L. (1767 : 1061) [redet. *Sphaeroma serratum* (Fabricius, 1787)]

Oniscus asellus L. (1758 : 637)

Oniscus armadillo L. (1758 : 637) [redet. *Armadillidium vulgare* (Latreille, 1804)]

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Conchoecia hystrix n. sp. a new halocyprid ostracod for the Porcupine Bight region of the Northeastern Atlantic

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Introduction

During *Discovery* cruise 105 investigations were made into the influence of the proximity of the sea-bed on the midwater fauna on the continental slope just south of the Porcupine Sea Bight off south-west Ireland in the Northeastern Atlantic. Samples were collected to within 15 m of the seabed at four stations over soundings ranging from about 1000–1650 m using a multiple RMT 1 + 8 system (Roe & Shale, 1979). Height above the bottom was measured by the reflection of the sound signal from the net monitor used to control the opening and closing the nets and to telemeter back to the ship the depth of fishing, net speed and the *in situ* temperature.

Each set of samples included a series of three successive samples of a plankton net with a nominal 1 m² mouth area and a mesh size of 0·33 mm, and a micronekton net with a nominal mouth area of 8 m² and a mesh size of 5 mm. Each successive sample was fished closer and closer to the sea bed. Since the soundings varied along the ship's track, the nets were kept within a constant range of the sea bed.

Initial analysis of the planktonic ostracods has revealed the presence of a new species of halocyprid ostracod that fits the old concept of the genus *Conchoecia* (sensu Müller, 1906), but does not fit any of Müller's groupings. Poulsen (1973) has recently subdivided the genus *Conchoecia,* but as many of his new genera are heterogenous, and since no type species were designated (Martens, 1979), this new species is described here as *Conchoecia hystrix.*

Conchoecia hystrix n. sp.

The specific name is derived from the latin name for the porcupine after the name of the type locality.

The holotype, a male was taken at *Discovery* station 10108 (station details in Table 1). It is mounted in 'Euparal' on slides in the British Museum (Natural History) No. 1980. 132.

MALE. The holotype has a carapace length of 1·23 mm and the only other male specimen taken, also at the type locality, was 1·26 mm long. The breadth of the carapace is equal to its height, and a little less than half its length (Table 2). Viewed laterally the carapace tapers anteriorly (Fig. 1A) with the ventral edge curving smoothly into the posterior edge. Viewed ventrally (Fig. 1B) the sides of the carapace curve smoothly. There are no spines at the posterior dorsal corner and there is an absence of sculpturing. The asymmetric gland on the left valve opens just posterior of the posterior hinge, but just dorsal to the male dorsal glands. Three groups of small edge glands with granular contents open on the right valve between the opening of the asymmetric gland and the posterior ventral corner, and there are corresponding groups of similar but slightly larger glands on the left valve (Fig. 1C).
Frontal organ The stalk of the frontal organ or Organ of Bellonci (Andersson, 1977) ends level with the end of the limb of the first antenna (Fig. 1D). The capitulum is bare of armature. It is downturned with a broad base which initially tapers rapidly but the distal two thirds are parallel-sided. The tip is rounded.

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Table 1 Station data and length data for all the specimens of *Conchoecia hystrix* collected on *Discovery* cruise 105.

Station 10108 haul 8 RMT 1 (Net 3) start position 49°23·6'N 12°47·6'W
    Depth of fishing   1410–1425 m (15–30 m above sea bed)
    Date   6 September 1979 1347–1420 hours. Distance travelled by net 1·39 km
    ♀♀   1·34 (mounted specimen), 1·36, 1·32, 1·32, 1·38, 1·38, 1·42, 1·32, 1·32, 1·38, 1·34 mm
    ♂♂   1·23 (holotype), 1·26 mm
    Stage VI   1·02, 1·02, 1·02, 1·04, 1·06, 1·08, 1·10 mm
    Stage V   0·78, 0·84 mm
    Stage IV   0·66 mm

Station 10108 haul 7 RMT 1 (Net 2) start position 49°25·4'N 12°49·1'W
    Depth of fishing   1350–1410 m (30–90 m above sea bed)
    Date   6 September 1979 1247–1347 hours. Distance travelled by net 3·73 km
    ♀♀   1·34, 1·38 mm

Station 10110 haul 5 RMT 1 (Net 3) start position 49°17·0'N 11°50·8'W
    Depth of fishing   935–1000 m (15–40 m above sea bed)
    Date   7 September 1979 2224–2324 hours. Distance travelled by net 2·37 km
    Stage VI   1·02 mm

Table 2 Meristic characters of the carapaces, frontal organs and first and second antennae of the male holotype and female paratype expressed as percentages of the total carapace length.

	♂	♀
Carapace length mm	1·23	1·34
Carapace breadth	47·8	41·1
Carapace height	47·8	52·1
Frontal organ stalk	40·7 ⎫	35·0
capitulum	19·0 ⎬	
Ant. 1 Segt 1	18·2	–
Segt 2	18·2	–
Total	36·5	17·3
dorsal seta	–	2·0
a	23·9 ⎫	
b	49·5 ⎬	17·7
c	6·5 ⎭	
d	45·1	
Ant. 2 Protoprodite	48·6	40·6
Exopodite segt 1	20·8	19·0
Exopodite segt 2–8	9·6	8·7
Longest swimming seta	49·4	45·3
Endopodite seta f	51·2	35·9
Endopodite seta g	38·1	30·3
Endopodite setae h, i, j	16·4	24·6–30·3

First antenna (Fig. 1D)   The first two segments are subequal and bare. The dorsal seta on the second segment that holds the stalk of the frontal organ in place is inserted just over a third of the way from the segment's proximal end. The a seta is long and reflexed back parallel to the limb and almost extends to its base. The c seta is short. The e seta is only slightly longer than the d and b setae, and carries two rows of alternating spines with 20–21
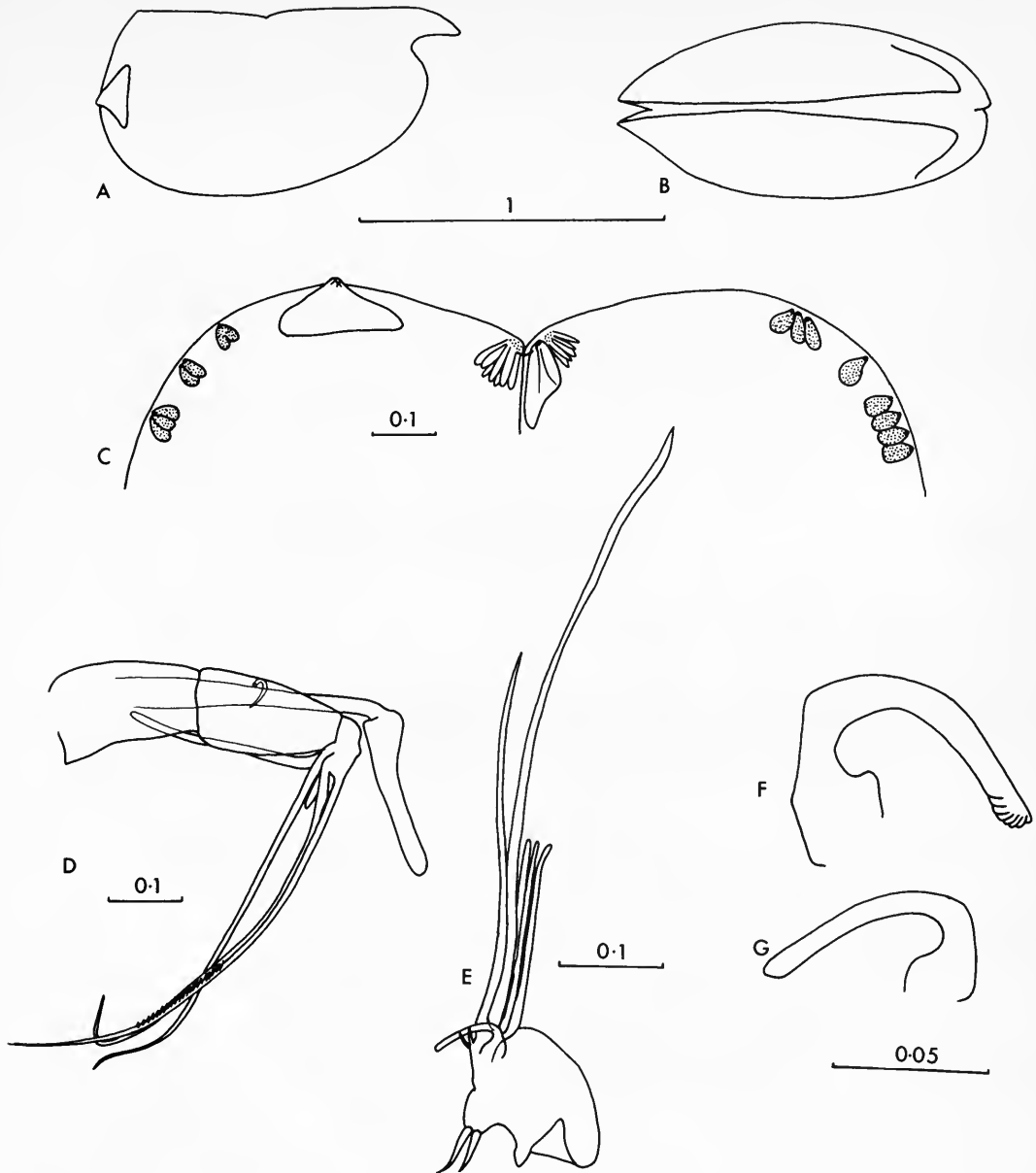
Fig. 1 *Conchoecia hystrix* male holotype. A. Outline of carapace lateral view. B. Outline of carapace ventral view. C. Detail of the carapace glands viewed from the outside showing the asymmetric gland on the left valve opening posterior of the hinge and its position relative to the openings of the male dorsal corner glands, and also the distribution of the edge glands with granular contents. D. Frontal organ and first antenna. E. Endopodite of the left second antenna. F. Hook appendage of the right second antenna. G. Hook appendage of the left second antenna. Scales in millimetres.

spines in each row. There is some suggestion of a weakly developed pad on the b seta, otherwise both the b and d setae are bare.

Second antenna   The protopodite is just less than 50% of the carapace length and similar in length to the longest swimming seta. The f seta on the endopodite is slightly longer and is nearly 4/3's the length of the g seta and three times the lengths of the h, i and j setae. All these
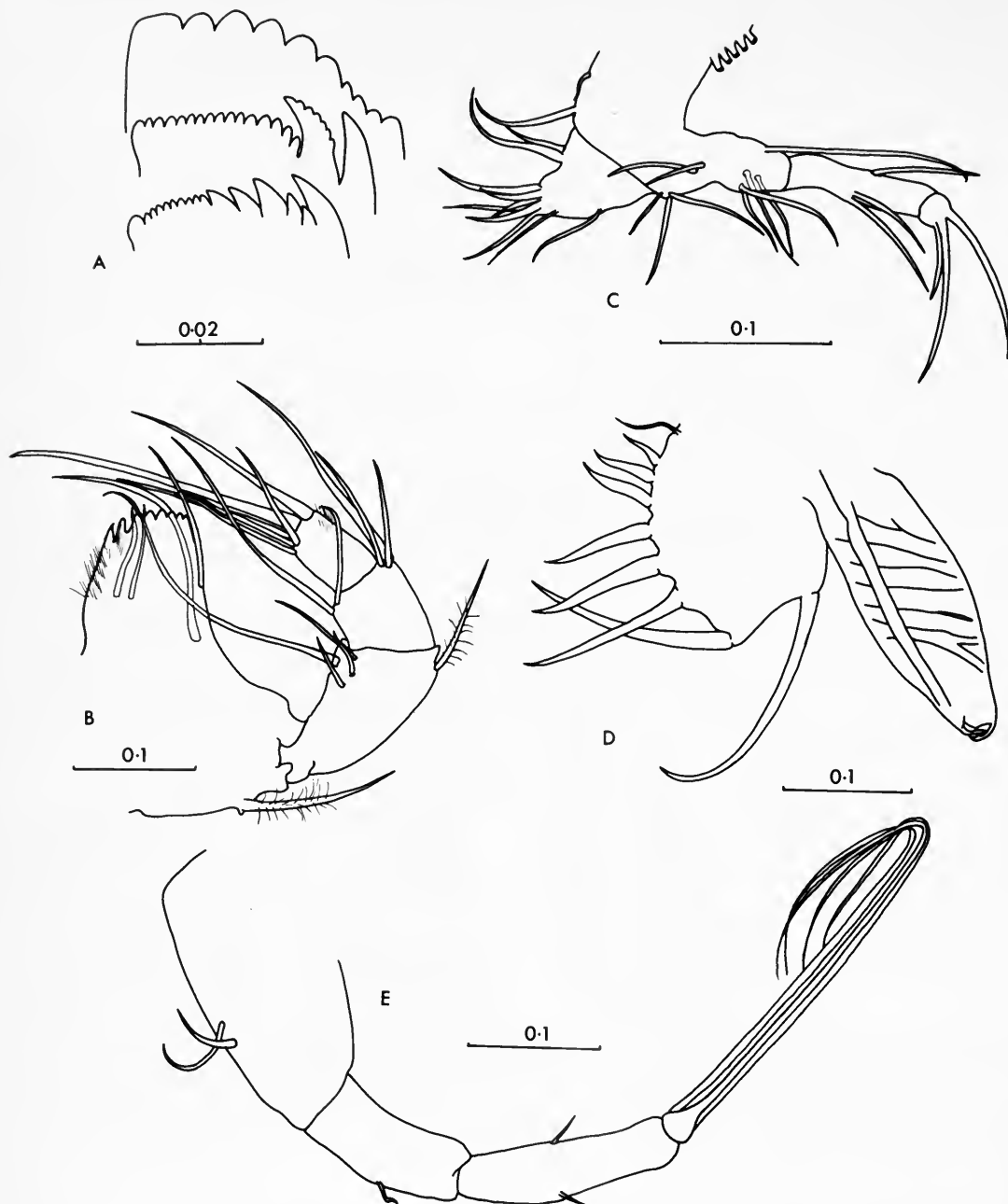
Fig. 2 *Conchoecia hystrix* male holotype. A. Toothed edge of the coxale and tooth lists of the mandible. B. Basale and endopodite of the mandible. C. Fifth limb. D. Caudal furca and copulatory appendage. E. Sixth limb. Scales in millimetres.

setae are bare. The a and b setae are also bare (Fig. 1E). The hook appendage on the right endopodite (Fig. 1F) has a short straight basal part, followed by a right angle bend and a slightly tapering curved arm which has a ridged rounded end. The left hook appendage (Fig. 1G) is a much weaker structure lacking the marked right angle bend and the ridging on its tip.

Mandible   The first segment of the exopodite (Fig. 2B) carries two long setae and two very short setae on its inner face. The longest terminal claw seta is nearly as long as the total length of the exopodite. The toothed edge of the *pars incisa* is normal for the genus. There are rows of hairs in the region below the two spine teeth. The coxale toothed edge consists of ten teeth (Fig. 2A). The distal list has two large teeth, the second of which has secondary serrations, followed by 17–18 small less well defined teeth. The proximal list has a large tooth followed by two smaller teeth, another large tooth and a further fifteen teeth that become progressively smaller. The inner toothed surface, used by Poulsen (1973) as one of the main criteria for separating his genera, appears to be undivided.

Labrum   It is slightly notched, although the type specimen appears to have an aberrant structure.

Maxilla   The basal segment (Fig. 3E) carries a seta. The first endopodite segment has six anterior, one lateral and three posterior setae.

Fifth limb   The first segment of the exopodite (Fig. 2C) has a group of three setae ventrally near its base, and a further two setae inserted laterally on its outer face. A further two setae occur ventrally towards its distal end together with a lateral seta on both the inner and outer faces. There is also a long dorsal seta which extends to the tip of the limb. The second segment has one dorsal and two ventral setae. The most ventral of the terminal claw setae is relatively short and thin.

Sixth limb   The basal segment (Fig. 2E) carries two very small setae. The second segment has a single ventral seta and the third segment one seta on both dorsal and ventral surfaces.

Caudal Furca   The furca (Fig. 2D) carries the normal eight claw setae for the genus with a dorsal unpaired seta. The first claw setae are more curved than usual.

Copulatory organ   The organ (Fig. 2D) tapers towards its rounded end. There are about five bands of oblique muscles.

FEMALE. The female paratype has a carapace length of 1·34 mm. It, too, is mounted on slides in 'Euparal' and deposited in the British Museum (Natural History) No. 1980. 133. The range in length of the other thirteen specimens is 1·32–1·42 mm, averaging 1·35 mm. The carapace shape (Fig. 3A, B) is similar to that of the male's, although the height is relatively greater and the breadth relatively slimmer. The positions of the asymmetrical glands are similar to the male, and there is the same distribution of edge glands with granular contents. There is a faint longitudinal sculpturing on the carapace of some specimens.

Frontal organ   The capitulum is not well differentiated from the stalk (Fig. 3C), but it is bent down very slightly. The ventral and lateral surfaces of the capitulum are covered with short spines. The tip of the capitulum is produced into a spine. The whole organ is about twice the length of the limb of the first antennae.

First antenna   The limb is not well differentiated into segments (Fig. 3C) and it is bare of supplementary armature. There is a very short dorsal seta which does not even reach the end of the limb. The a–d setae are half the length of the e seta, which is about a third the carapace length. The e seta carries a few relatively long distally pointing spinules on its trailing edge half way along its length, and a scatter of similar spinules more distally on the leading edge.

Second antenna   The protopodite (Fig. 3D) is around 40% of the total carapace length. It carries a patch of hairs close to the insertion of the endopodite. The first exopodite segment is just less than half the length of the protopodite and just over twice the length of the other exopodite segments. The longest swimming seta is a little longer than the protopodite.

On the endopodite the a and b seta are bare. There are no c, d or e setae. The f seta which is equal in length to the protopodite, is bare but is slightly flattened distally. The g seta is similar in structure and length to the h, i and j setae.

Gut contents   The gut contents included a multilayered block of folded membranous material of unidentifiable origin. The contents were rich in densely staining granules that appeared to be coccoid bacteria about 1 μm in diameter. It also included a few rounded mineral particles 2–4 μm in size, suggesting the species may feed on the sea bed.
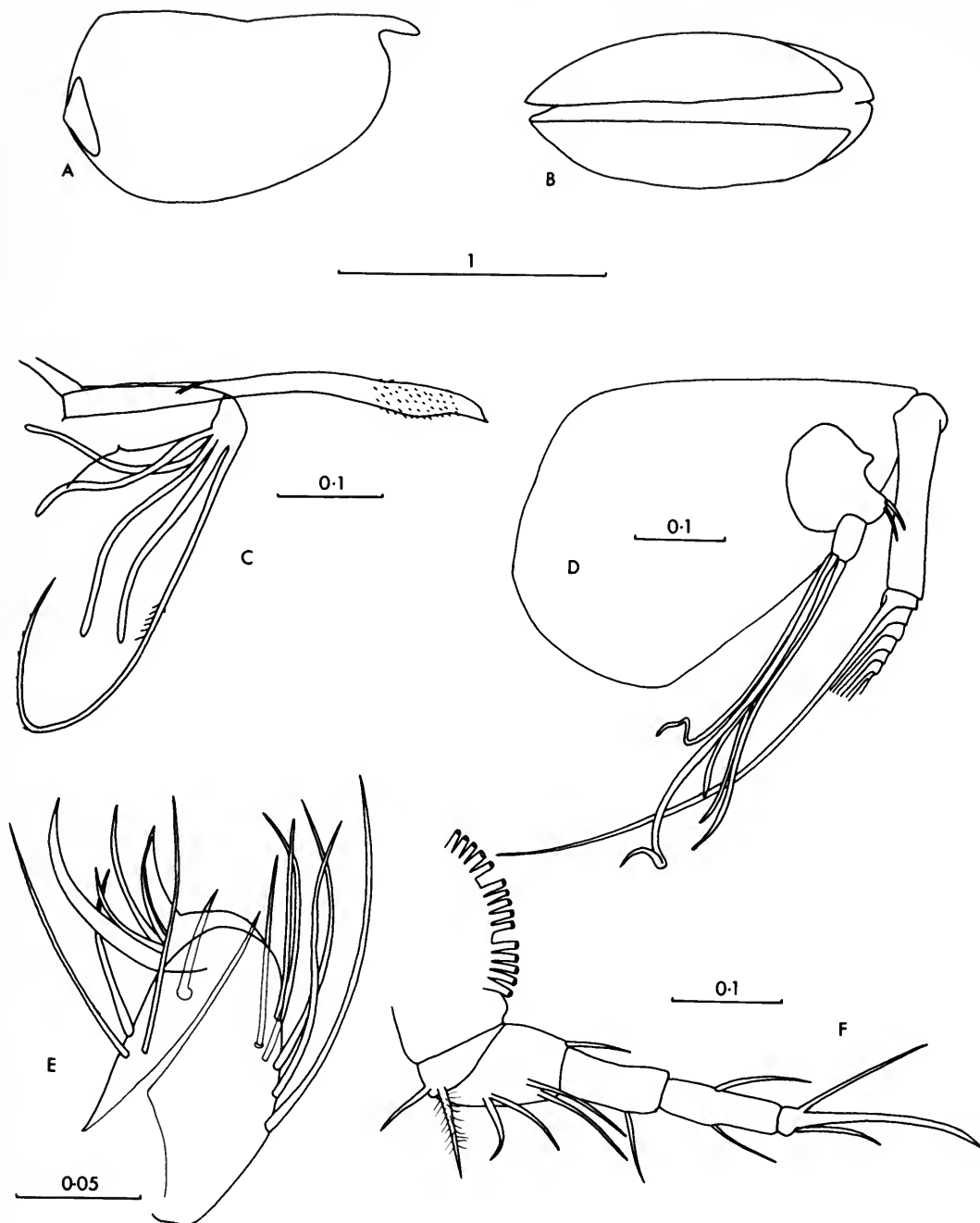
Fig. 3 *Conchoecia hystrix* female paratype. A. Carapace lateral view. B. Carapace ventral view. C. Frontal organ and first antenna. D. Second antenna. E. Endopodite of maxilla. F. Sixth limb. Scales in millimetres.

DISCUSSION. The depth range of this species appears to be restricted. It was absent from samples collected at depths of 1600–1700 m and only a single specimen was taken at a shallower depth than at the type locality. The occurrence of novel species close to the sea bed even in relatively shallow depths suggests that there are distinct environmental conditions in this poorly explored habitat (e.g. Wishner, 1980).

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The *Conchoecia skogsbergi* species complex (Ostracoda, Halocyprididae) in the Atlantic Ocean

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Introduction

The planktonic ostracod genus *Conchoecia* includes a heterogeneous array of 105 described species with at least another 15–20 recognized, but as yet undescribed (Angel, personal communication). The named species have been separated into a number of groupings (Müller, 1906*a*; Skogsberg, 1920). Some of these were given generic status by Granata & di Caporiacco (1949) and Poulsen (1973) but this nomenclature is not universally accepted because several of the genera appear to be unnatural units (Angel and Fasham, 1975 : 711). One of the more important, and probably natural, assemblages is the *rotundata* group (= *Metaconchoecia* Granata & di Caporiacco, 1949), which comprises 11 or 12 previously described species, most obviously united by the location of the left asymmetric gland in an anterior position, just behind the rostrum.

Although most of the *rotundata* group species are fairly well understood, two names, *C. rotundata* Müller, 1890 and *C. skogsbergi* Iles, 1953, have not been applied consistently. *C. rotundata* has been the subject of particular confusion. These long standing taxonomic problems have been compounded in recent years by Angel's recognition that '*C. rotundata*' in Atlantic *Discovery* material comprises an array of very similar 'forms' (Angel, 1972; 1979 : 68–73; Angel & Fasham, 1975 : 711). In the present paper, which is largely based on the same *Discovery* material, *C. rotundata* and *C. skogsbergi* are redescribed and eight new species are established. All but one of these ten species are embraced by Angel's '*C. rotundata* forms 1–15'. They together make up a closely related assemblage within the *rotundata* group which is referred to here as the *skogsbergi* complex.

It is obvious from material in other collections that many, perhaps all, of the *skogsbergi* complex species were seen by earlier workers. Understandably, they were usually identified as *C. rotundata* or, in more recent literature, as *C. skogsbergi*.

Materials and methods

Most of the material was collected by the RRS *Discovery* between 1968 and 1974 in the N. Atlantic at a series of stations situated approximately along the 20°W meridian between 60°N and the equator (Angel & Fasham, 1975) and also along a 32°N transect from Africa to Bermuda (Angel, 1979). With a few exceptions, these samples were taken with the RMT 1 component of the RMT 1 + 8 opening and closing net system which is able to sample discrete horizontal horizons within the water column (Baker, Clarke & Harris, 1973). The gear was usually fished at four depth horizons down to 100 m, then 100 m horizons down to 1000 m and broader bands between 1000 m and 2000 m, thus allowing reasonably precise data on the depth distribution of planktonic organisms to be obtained. Further details of sampling procedures with the RMT 1 + 8 are given elsewhere (Angel & Fasham, 1976; Badcock & Merrett, 1976; Angel, 1979). At *Discovery* Station 6665, a modified Indian Ocean Standard Net (N113) fitted with a catch dividing bucket (CDB, Foxton, 1963) was used. A smaller number of specimens from the S. Atlantic and the Atlantic sector of the Southern Ocean

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were collected by *Discovery* II between 1936 and 1938 with vertically hauled 70 cm nets (N70V). The station data are deposited in the library of the British Museum (Natural History). The *Discovery* material of Iles (1953), the remaining specimens of which have been reexamined, was collected from the RRS *William Scoresby* with N70V nets.

Some important museum material from the Atlantic, Indian, Pacific and Southern Oceans, including specimens studied by G. W. Müller, Skogsberg, Fowler and Poulsen, was reexamined. However, a comprehensive examination of all relevant material in other collections was not attempted. Details of this material are given below and in Tables 1 & 2 and Appendix 1. The following abbreviations are used when referring to examined specimens:

BM(NH)   –British Museum (Natural History), London.
DC, Wormley   –*Discovery* Collections, Institute of Oceanographic Sciences, Wormley, U.K.
NR, Stockholm   –Naturhistoriska riksmuseet, Stockholm, Sweden.
SI, Washington   –Smithsonian Institution, Washington, D.C., U.S.A.
ZIZM, Hamburg   –Universität Hamburg, Zoologisches Institut und Zoologisches Museum, Hamburg, Federal Republic of Germany.
ZM, Copenhagen   –Zoologisk Museum, Copenhagen, Denmark.
ZM, Berlin   –Zoologisches Museum, Berlin, German Democratic Republic.
S.A.E.   –Swedish 'Antarctic' Expedition 1901–1903.

In the laboratory, the ostracods were examined, measured and dissected under a Wild M5 Stereomicroscope. Mounted animals were examined under a Wild M15 microscope. Carapace outlines were executed with the aid of an M5 'Zeichentubus' and the line drawings of appendages with an M15 'Zeichentubus'. Carapace lengths and breadths were measured with the animal lying on its back. In the text, mean carapace lengths are given with their standard deviations. Potentially ambiguous measurements are defined by Gooday (1976 : 59).

The following abbreviations for morphological characters are used:

A1	First antenna
A2	Second antenna
Ex1, 2 etc.	First, second etc. segment of exopodite
En1, 2 etc.	First, second etc. segment of endopodite
LSS	Longest swimming seta
F.O.	Frontal organ
L	Carapace length
H	Carapace height
B	Carapace breadth
LAG	Left asymmetric gland
RAG	Right asymmetric gland

Historical Review

(i) *1890–1920. Conchoecia rotundata* was established by Müller (1890), in the earliest of his halocyprid papers, on the basis of a few specimens taken at a depth of 1000–4000 m of wire at two stations in the tropical Pacific. These specimens were up to 1·15 mm long. They were inadequately described and the species cannot now be recognized with any confidence, although its identity is speculated on below. A few years later, Müller (1894) gave a fuller

description of a smaller form (L = 0·80 mm) from the Mediterranean which had a more rounded lateral outline. The situation becomes further confused with Müller's (1906*a*) *Valdivia* report in which specimens of *C. rotundata,* collected over a wide area (40°N to 62°S in the Atlantic, Indian and Southern Oceans), were said to vary considerably in size and outline with height : length ratios of 4/7 (57·1%) to 8/19 (42·1%) and lengths of 1·40 mm to 1·75 mm for Antarctic specimens and 0·80 mm to 1·40 mm for those from warmer water. Müller (1906*a* : 83, pl. XVII, figs 23–26) distinguished two distinct carapace types in the *Valdivia* material, one long and elongate and the other relatively short and more rounded, the latter corresponding closely to the Mediterranean form (Müller, 1894) of *C. rotundata.* The same author gives additional records of *C. rotundata* in his *Siboga* and *Gauss* reports (Müller, 1906*b*, 1908) but in neither of these papers is the material described. The account of this species in Müllers (1912) comprehensive treatise on the Ostracoda is drawn from the description in the *Valdivia* report. It is shown below that Müller's *Gauss* and *Valdivia* specimens, at least, belong to a number of species and his published descriptions (Müllers, 1906*a*, 1912) of '*C. rotundata*' greatly oversimplify the nature of this material.

In an unorthodox but stimulating contribution to halocyprid taxonomy, Fowler (1909) recognized the taxonomic difficulties created by Müller's inclusion of two widely different forms in one species. Fowler believed both forms were present in his material from the Bay of Biscay and resolved the problem by regarding the elongate carapaces as adults (Stage I) and the short carapaces as penultimate instars (Stage II) of the same species. The Stage I instars had mean lengths of 1·0 mm (♂) and 1·1 mm (♀), the Stage II instars had mean lengths of 0·75 mm (♂) and 0·79 mm (♀) (Fowler, 1909 : 273). It is significant that these temperate specimens of the elongate form were markedly smaller than Müller's (1906*a*) elongate form from the Southern Ocean, a point returned to below.

This initial period of research ended when Skogsberg (1920) described 24 specimens of *C. rotundata* from the SW Atlantic, ranging in length from 1·45 mm to 1·60 mm (both sexes). These correspond well in size and lateral shape to Müller's (1906*a*) long form. With characteristic thoroughness, Skogsberg (1920) reviewed the *C. rotundata* problem and concluded that the long and short forms were distinct taxonomic entities, the short form, of which he had no material, perhaps being the same as *C. nasotuberculata* Müller, 1906, and the elongate form being closer to Müller's original concept of *C. rotundata.*

(ii) *Iles' contribution.* One of the key contributions was that of Iles (1953) who studied *Discovery* samples from the Benguela Current in the SE Atlantic. In many of these samples, Iles identified both adults and juveniles of the long and short forms of *C. rotundata* as well as *C. nasotuberculata.* Iles noted that the long and short forms in his material were morphologically quite distinct and also had different depth distributions. He therefore concluded that Skogsberg (1920) had been correct in suspecting that the long and short forms of Müller (1906*a*) and Fowler (1909) were separate species. Iles believed that the short form was conspecific with the Mediterranean *C. rotundata* of Müller (1894) because of its similar size (L = 0·80–0·90 mm) and lateral carapace outline. In addition, he pointed out that despite Müller's (1890) inadequate description, there were sufficient differences between the short form and Müller's original concept of *C. rotundata* to justify describing it as a distinct species, *C. teretivalvata* Iles, 1953. A second new species, *C. skogsbergi,* was erected for the long form, which clearly differed in size and lateral outline from the original *C. rotundata.* However, Iles (1953) did not describe the Benguela Current material of *C. skogsbergi* but referred to Skogsberg's (1920) account of *C. rotundata* from the SW Atlantic as the type description. Following Iles (1953) report, *C. rotundata* was then left as the name of a valid but unrecognizable taxon which included only Müller's (1890) specimens.

(iii) *1967 onwards.* Despite the unresolved nature of *C. rotundata,* the taxonomic legacy left by Skogsberg and Iles appeared to be fairly satisfactory in that two species, *C. skogsbergi* and *C. teretivalvata,* both previously identified as *C. rotundata,* were now clearly recognized as distinct and were adequately described. This was the situation when the lull in planktonic

ostracod studies, which followed the publication of Iles (1953) paper, was terminated in the late 1960s. During this most recent and continuing period of research, both of Iles (1953) species have been widely recognized. There are records of *C. skogsbergi* from the following high latitude areas in the northern hemisphere: the Norwegian Sea (Angel, 1968*a*), near the North Pole (Leung, 1972; 1973), the Bering Sea (Chavtur & Shornikov, 1974), the Okhotsk and Bering Seas and the Kurile-Kamchatka trench (Chavtur, 1976; 1977*a*; 1977*b*). In the Southern Ocean it has been recorded by Hillman (1967; 1968; 1969; as '*C. rotundata*') and Deevey (1974; 1978*b*). These recent, cold water, high latitude reports of *C. skogsbergi* are fairly convincing since where descriptions, or at least length data, are given, the specimens conform more or less closely to Skogsberg's (1920) definitive description.

C. skogsbergi has also been reported from warmer, temperate, and tropical waters but here the situation is more complex and probably none of these identifications is correct. Angel's recent studies of N. Atlantic *Discovery* material have revealed an array of undescribed ostracod species, closely related to *C. skogsbergi* but smaller, although generally larger than *C. teretivalvata*. Angel & Fasham (1975; see also Angel, 1972; 1977*a*; 1977*b*; 1979) distinguished 15 forms within this complex. In the present study, which is largely based on the same material, Angel's forms are placed in nine species, seven of them new. Some of these *skogsbergi* complex species are the same as those assigned by other authors to *C. rotundata* or low latitude forms of *C. skogsbergi*. The male *C. rotundata* long form of Fowler (1909: pl. 24, fig. 205) belongs to Angel & Fasham's (1975) form 3 while the smaller, warmer water variety of *C. skogsbergi* reported by Deevey (1968; 1974; 1978*a*) from the Sargasso Sea, the Atlantic between 30°S and 35°S and from off Venezuela, is at least in part equivalent to forms 1, 5 and 13. From the same area Deevey (1968) described, as *C. rotundata*, a small form which also belongs to this complex (form 15). The rather different species from the W. Atlantic and tropical Pacific assigned to *C. rotundata* by Poulsen (1973), is close to form 4. Another species, said to be distinct from both *C. skogsbergi* and *C. teretivalvata*, was reported by George (1969) and George, Purushan & Madhupratap (1975) from the NW Indian Ocean but was not described and so cannot be assessed; the same comment applies to *C. rotundata* of Chavtur (1977*a*) from the subtropical Pacific.

The *C. rotundata* material of G. W. Müller

Several fairly large collections of G. W. Müller's material still exist (Athersuch, 1976). During this study, animals collected by the *Valdivia* (Deutsche Tiefsee-Expedition 1898–1899; 642 specimens: see Müller, 1906*a*) and the *Gauss* (Deutsche Süd-Polar Expedition, 1901–1903; 617 specimens: see Müller, 1908), and identified by Müller as *C. rotundata*, were examined. These specimens are from the Atlantic, Southern and Indian Oceans. None are from the Pacific. It was not possible to examine the Bay of Naples samples (Müller, 1894) mentioned by Athersuch (1976). The *Valdivia* and *Gauss* material is all preserved in alcohol. In general, the *Valdivia* specimens are poorly preserved with the valves widely splayed, often making identification impossible, or at best tentative. The *Gauss* material is generally in better, often surprisingly good condition and most specimens can be identified.

The 20 or so species found in these samples are listed in Tables 1 and 2 and Appendix 1. About half of them (*C. brachyaskos* Müller, 1906, *C. elegans* Sars, 1865, *C. hyalophyllum* Claus, 1890, *C. kyrtophora* Müller, 1906, *C. macrochiera* Müller, 1906, *C. macromma* Müller, 1906, *C. nasotuberculata*, *C. procera* Müller, 1894, *C. pseudoparthenoda* Angel, 1971 (very close to *C. parthenoda* Müller, 1906) and *C. spinirostris* Claus, 1974) are each represented by only a few specimens and were probably simply misidentified by Müller. The remainder comprise *C. arcuata* Deevey 1978, *C. rotundata* sensu Deevey, 1968, *C. skogsbergi*, *C. teretivalvata* and five of the new species described herein, all of which were presumably embraced by Müller's understanding of *C. rotundata*. These nine species, although closely related, differ from each other to varying degrees and in some cases are rather strikingly different (for example *C. skogsbergi* and *C. teretivalvata*). It is therefore

somewhat surprising that Müller was content to leave them unseparated. However, when examining his samples, for example the one from *Gauss* Station 12.11.01 which contains 196 specimens belonging to nine different species (Table 2), one senses that he was exasperated by the diversity of closely related species within '*C. rotundata*' and chose (Müller, 1906*a*, 1912) not to proceed beyond dividing this 'species' into long and short forms.

The present status of *C. rotundata* and *C. skogsbergi*

Following the historical review and the discussion of Müller's material, we are now in a position to consider how the names *C. rotundata* and *C. skogsbergi* are applied in this paper.

Müller's (1890) original description of *C. rotundata* includes the following taxonomically useful information. The carapace is moderately elongate and strongly tapered with the greatest height somewhat > half the length; the posterior end is strongly curved with the extremity at about half the height; the maximum breadth is somewhat < half the length; the length is up to 1·15 mm; the frontal organ capitulum is of somewhat variable shape; there are ten pairs of spines on the male first antenna e seta. Müller also illustrates a side view of the female carapace, the female second antenna endopodite, the male first antenna e seta armature and two male and two female frontal organ capitulums. As pointed out above, this information, together with the figures, is not sufficient to allow the species to be identified. However, it is possible to speculate. The lateral outline (Müller, 1890: pl. XXVIII, fig. 42) is reminiscent of several *skogsbergi* complex species, although less elongate than any of them. On the other hand, the outline is more elongate than in *C. kyrtophora, C. nasotuberculata* and *C. teretivalvata* and these three species are also smaller (< 1·0 mm) than the largest of Müller's (1890) specimens. The male e seta spines (pl. XXVIII, fig. 43) resemble these spines in the *skogsbergi* complex but are unlike those of *C. kyrtophora.* On the other hand, one of the female and one of the male frontal organ capitulums (pl. XXIX, figs 14a, d) are closely similar to the capitulum in *C. kyrtophora* and some related *rotundata* group species, while the other two capitulums (pl. XXIX, figs 14b, c) are more reminiscent of this structure in the *skogsbergi* complex species. It is therefore likely that Müller (1890) had at least two species in his material, perhaps *C. kyrtophora* and a species of the *skogsbergi* complex.

Müller's Pacific types of *C. rotundata* are presumed lost but, as discussed above, the *Gauss* and *Valdivia* material of this 'species' includes a variety of species, many of them belonging to the *skogsbergi* complex. None of this material is from the Pacific and it can therefore cast no direct light on the original identity of *C. rotundata.* However, it does demonstrate that Müller (1906*a*, 1908) had a very broad concept of *C. rotundata* when writing the *Valdivia* and *Gauss* reports and adds weight to the above suggestion that this species was originally polytypic.

Since there is no clear idea of what Müller (1890) meant by *C. rotundata,* the name is applied here in the sense of Deevey's (1968). There are, admittedly, some clear discrepancies between Deevey's species and Müllers (1890) original account of *C. rotundata.* Müller's specimens were considerably larger and the lateral outline, although similar, was relatively higher; also the male first antenna e seta (Müller, 1890: pl. XXVIII, fig. 43) had more spines (20). Several of the new *skogsbergi* complex species are closer to Müller's (1890) specimens in size and lateral outline and may be better candidates for this name. However, less confusion will be caused if the name is retained for Deevey's species which is now adequately described and well understood. This pragmatic approach is further justified by the presence of *C. rotundata* sensu Deevey in Müller's Gauss material.

C. skogsbergi presents rather different problems. As outlined above, Iles established the species after studying specimens from the Benguela Current which convinced him that the long form (*C. skogsbergi*) and the short form (*C. teretivalvata*) of *C. rotundata* were distinct species. However, Iles did not actually describe the Benguela specimens that he referred to *C. skogsbergi* but directed the reader to Skogsberg's (1920) description and figures which 'may

be taken as typical for this species'. This statement is followed by the sentence 'Type material will be deposited at the British Museum' (Iles, 1953 : 265), but in fact there are no specimens of *C. skogsbergi* in the BM(NH) collections. In July 1976, Dr Iles kindly sent me his remaining Benguela Current material of *C. skogsbergi*. It included a dissected male, mounted on two slides, each labelled 'type'. However, the slides did not have a catalogue number and were clearly not part of a museum collection.

Since the Benguela Current material was not described, since the type specimens selected from it were not deposited in a museum and since the type description was said to be Skogsberg's (1920) account of the long form of *C. rotundata,* the species should clearly be based on Skogsberg's material. I therefore obtained, through the courtesy of Dr R. Ölerod, Skogsberg's remaining material of *C. rotundata* in the Naturhistoriska riksmuseet, Stockholm, and selected a type specimen from it.

This procedure, apart from being nomenclaturally correct, has the advantage of basing *C. skogsbergi* firmly on a typical specimen from the SW Atlantic, rather than on the undescribed material of Iles (1953). In fact, Iles specimens have proved, on reexamination, to belong to another of the *skogsbergi* complex species and hence additional nomenclatural confusion has been avoided.

Taxonomic characters

For the purpose of routinely identifying planktonic ostracods, it is obviously an advantage if the important taxonomic characters are external features of the carapace, rather than appendage details which require dissection to be seen. It is therefore fortunate that in the *skogsbergi* complex, and probably in the genus *Conchoecia* as a whole, speciation seems always to be expressed morphologically in the size and shape of the carapace. The disposition and armature of the limb segments, and other internal features are, on the other hand, relatively conservative. With experience, and reasonable preservation, the species described here can therefore be recognized by their external morphology, although examination of the limbs is occasionally essential to confirm an identification. In this section, the taxonomically important carapace characters, and some less important internal characters, are discussed.

(i) *Carapace outline.* In material which is reasonably undistorted, species can usually be separated by consistent, although sometimes subtle, differences in their lateral and ventral outlines. In lateral view, particular attention should be paid to the relative height of the carapace, the way it tapers, the curvature of the posterior end and the position, above or below the mid-point, of the posterior extremity. In ventral view, the relative breadth of the carapace, the curvature of the sides and the shape of the anteroventral region, which may be sharply or bluntly pointed, are important. The ventral appearance of the carapace should always be illustrated. There is often some intraspecific variability in the carapace outline, for example in the degree to which specimens taper in lateral view. To show the range of variation, a series of carapaces are illustrated for each of the species described in the paper.

(ii) *Carapace length.* Certain closely related species of *Conchoecia* can be readily distinguished because their size ranges do not overlap (Angel, 1973; Gooday, 1976). This is not usually the case in the *rotundata* group, most species of which have overlapping size ranges. However, considering the *skogsbergi* complex by itself, two species do have characteristic carapace lengths: *C. rotundata* is consistently smaller, and *C. skogsbergi* is usually larger than other species. As shown below in the key, carapace length data may also be of value in separating similar species. Measurements of material spanning the known range of each species often reveal slight, geographically related size variations, lengths usually tending to decrease southwards. These complete data on the geographical variation in carapace length are available in tables stored in the BM(NH) library.

(iii) *Position of the left asymmetric gland.* In the *rotundata* group, the position of this gland varies from <9% (*C. nasotuberculata*) to >25% (*C. glandulosa* Müller, 1906, *C. macromma*) of the carapace length behind the tip of the rostrum, but does not uniquely characterize any of the species. Gland positions for the *skogsbergi* complex species are summarized in Table 9. In one of these species the gland is situated more posteriorly than in another member of the complex. The gland position may also be of value in discriminating between closely related species.

(iv) *Other morphometric characters.* The relative lengths of the frontal organ capitulum and the antennal segments and setae, expressed as percentages of the carapace length, have proved to be of taxonomic value in the genus *Conchoecia*. Within the *skogsbergi* complex, two species can be recognized using this character alone and pairs of species may also be separated in this way. However, the measurements are tedious and time consuming to obtain and although they may be used to confirm doubtful identifications, they are rarely of primary taxonomic importance.

(v) *Frontal organ capitulum.* This prominent structure is almost always described and illustrated in species descriptions and hence its usefulness as a taxonomic character needs to be considered. In the *rotundata* group it is of variable shape. The male capitulum of *C. glandulosa, C. kyrtophora, C. macromma, C. pusilla* Müller, 1906 and *C. nasotuberculata* is usually elongate, often slightly curved with a rounded, sometimes rather bulbous end. In the *skogsbergi* complex, and in *C. teretivalvata,* the male capitulum is relatively shorter and distally tapered, the ventral margin is clearly convex proximally and there is a corresponding, although less pronounced, concavity of the dorsal margin. In *C. isocheira* Müller, 1906 and *C. arcuata,* the male capitulum is rather similar to that of *skogsbergi* complex species. The female capitulum of *C. arcuata, C. isochiera, C. kyrtophora, C. macromma, C. nasotuberculata* and *C. pusilla* is not clearly delimited from the shaft, elongate, and rather bulbous distally, with a terminal spine in *C. macromma. C. glandulosa* has a similar, but more bulbous female capitulum. In the *skogsbergi* complex, and in *C. teretivalvata,* the female capitulum is more clearly delimited from the shaft, more or less tapered and the end pointed and downturned, or narrowly rounded and less clearly downturned. Hence, within the *rotundata* group, the shape of the capitulum may be characteristic of certain species, or species groupings.

Among members of the *skogsbergi* complex, the shape of the capitulum displays rather little interspecific variation. In males, the relative height may vary somewhat while the female capitulum is rounded in three species, pointed and clearly downturned in the remainder. Thus none of the species described in this paper has a characteristically shaped capitulum. Moreover, the shape sometimes varies within a species; this is particularly so in the case of *C. skogsbergi* (Figs 18, 19). For these reasons, the capitulum shape has very limited taxonomic value in the *skogsbergi* complex.

The number and the distribution of capitulum spines have been used as characters to separate *C. skogsbergi* and *C. rotundata* (Poulsen, 1973 : 73). However, the value of these spines as taxonomic characters was not confirmed during the present study.

(vi) *Armature of the male first antenna e seta.* This is another of the characters usually described by taxonomists. Among *rotundata* group species, *C. kyrtophora* is unique in having square ended spines lying at right angles to the seta (Angel, in press) and in *C. isochiera* the spines bear a single, distal row of 'moderately large, oval, hyaline appendage(s)' (Skogsberg, 1920 : 658). Müller (1912 : 62) used differences in the e seta armature to characterize these species in his key. All other members of the *rotundata* group have pointed, paired or staggered spines, lying almost flat against the seta. The number of these spines varies from 14 to 31 in the *skogsbergi* complex (Tables 5 & 13). However, the numbers show considerable overlap between species and are therefore of rather limited usefulness in taxonomy, although *C. rotundata* usually has fewer spines than the other members of the complex.

Key to the *Conchoecia rotundata* group (Figs 1–9, pp. 163, 171–174)

1. LAG > 20% of length behind tip of rostrum 2
   LAG < 20% of length behind tip of rostrum 4
2. Length usually < 1·25 mm (0·90–1·29 mm)* . . . . . . *macromma*
   Length usually > 1·25 mm 3
3. Anterior end curved and produced well forwards below rostrum; posterior end bluntly
   pointed where RAG opens above mid-point. L = 1·40–2·10 mm . . *glandulosa*
   Anterior end not produced forwards; posterior end smoothly curved. L = 1·60–1·85 mm
   (♂); 1·38–1·55 mm (♀) . . . . *abyssalis*
4. Length > 1·30 mm . . . . *skogsbergi*
   Length < 1·30 mm 5
5. Carapace short and round in lateral view; H > 60% of length 6
   Carapace more cylindrical; H < 50% of length 8
6. Sides of carapace evenly curved in ventral view. L = 0·80–1·15 mm . . *teretivalvata*
   Sides of carapace constricted behind insertions of A2 when viewed ventrally . . . 7
7. Carapace with lateral tubercles close to posterior dorsal corner. ♂ A1 e seta spines lie
   pointing dorsally, almost parallel to seta. LAG opens on rostrum, in front of anterior end of
   hinge . . . . *nasotuberculata*
   Carapace without tubercles. ♂ A1 e seta with spines set at right angles to seta. LAG opens just
   behind rostrum posterior to anterior end of hinge L = 0·72–1·0 mm . . *kyrtophora*
8. RAG situated below posterior dorsal corner, opening at end of triangular process
   which makes distinct angle in upper part of posterior margin 9
   RAG opens near posterior dorsal corner, not on a process so that posterior margin
   of carapace appears smoothly curved 10
9. ♂ A1 e seta bears single row of 7–9 spines, each bearing a distal hyaline appendage.
   L = 0·80–1·00 mm (♂), 0·95–1·11 mm (♀) . . . . *isochiera*
   ♂ A1 e seta bears about 16 simple paired spines. L = 0·70–1·13 mm . . . *pusilla*
10. Carapace with maximum height near middle, ventral margin arcuate; incisure tends to be
    deep and curved. ♂ A2 i and j setae with side branches. LAG > 15% of length
    behind tip of rostrum. L = 0·93–1·12 mm . . . . *arcuata*
    Carapace with maximum height nearer posterior end, lateral outline tapered with
    gently curved ventral margin; incisure tends to be fairly shallow. ♂ A2 i and j setae
    simple. LAG > 15% of length behind tip of rostrum in one species only 11
11. LAG > 15% of length behind tip of rostrum; in ventral view carapace narrow with B
    usually < 40% of length. On A1, b and d setae only slightly shorter than e seta.
    L = 0·95–1·18 mm . . . . *discoveryi* sp.n.
    LAG < 15% of length behind tip of rostrum; except in one species, carapace wider in
    ventral view, with B consistently > 40% of length; ♂ A1 b and d setae markedly shorter than
    e seta 12
12. LAG usually 12%–15% of length behind tip of rostrum. Posterior end strongly and
    symmetrically rounded or slightly downturned; in ♂ B = 38–42% of length. L > 1·06 mm
    (1·10–1·40 mm) . . . . *fowleri* sp. n.
    LAG perched above and just behind rostrum, < 12% of length behind tip; in ♂, B is always
    > 40% of length. Length < 1·20 mm 13
13. Carapace less strongly tapered, anteroventral region, below rostrum, is not sharply pointed
    in ventral view. Ventral outline not strongly biconvex. ♂A1 e seta with 23–28 spines . 14
    Carapace more strongly tapered, anteroventral region, below rostrum, is pointed in ventral
    view. Ventral outline more strongly biconvex. ♂ A1 e seta with 14–26 spines . . . 15
14. L = 1·06–1·26 mm. Posterior end asymmetrically curved in lateral view with extremity
    below the mid-point . . . . *wolferi* sp. n.
    L = 0·91–1·06 mm. Posterior end more symmetrically curved in lateral view with
    extremity around the mid-point . . . . *obtusa* sp.n.
15. Carapace unusually broad in ventral view, particularly in ♀; B > 50% (♂), > 46·0% (♀) of
    length. Length = 0·97–1·16 mm . . . . *inflata* sp.n.
    Carapace less broad in ventral view; except in one species, B < 50% (♂), < 46% (♀) of length 16

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*Although Deevey (1974) gives lengths of 1·50 mm (♂), 1·27–1·40 mm (♀) for *C. macromma*.

16. Length <0.87 mm ($\circ$), <0.83 mm ($\circ$); $\circ$ A1 e seta with 14–18 spines . . . ***rotundata***
    Length >0.87 mm ($\circ$), >0.83 mm ($\circ$); $\circ$ A1 e seta with 18–24 spines 17
17. Carapace height usually $>50\%$ of length; $\circ$ A1 LSS $>60\%$ of length, $\circ$ A2 LSS $>47\%$ of length. Length $= 0.98$–1.08 mm . . . . ***australis*** sp.n.
    Carapace height usually $<50\%$ of length; $\circ$A1 LSS $<60\%$ of length, $\circ$ A2 LSS $<47\%$ of length 18
18. Length $= 0.95$–1.20 mm. $\circ$ A2 f seta $>40\%$, g seta $>43\%$ of length; $\circ$ A2 LSS $>41\%$ f–j setae $>20\%$ of length . . . . ***subinflata*** sp.n.
    Length $= 0.85$–1.01 mm. $\circ$A2 f seta $<38\%$, g seta $<42\%$ of length; $\circ$ A2 LSS $<41\%$, f–j setae $<20\%$ of length . . . . ***acuta*** sp.n.

Systematic descriptions

Species of the *skogsbergi* complex show virtually no interspecific variation in the structure and setation of the mandible, maxilla, 5th, 6th and 7th limbs, labrum and caudal furca, or in the dentition of the mandibular tooth lists and cutting edge. The basic morphology of the first and second antenna in both sexes is also constant with only the proportional lengths of the main setae and segments (summarized in Tables 3, 4, 7, 8, 11, 12) and details of the setal armature (Tables 5, 13) varying between species. In the systematic section that follows, a complete account is therefore given only for *C. fowleri* sp. nov. and descriptions of other species are limited to those characters in which they differ morphologically from *C. fowleri* sp. nov. The description is not based on *C. skogsbergi* itself because the relatively large size and polytypic character of this species make it rather atypical of the *skogsbergi* group as a whole.

Most of the type material and other figured *Discovery* specimens are deposited in the BM(NH), under registration numbers 1979.690–827, 1980.141–145. There is also a collection of *Discovery* specimens of most of the described species deposited in the SI, Washington under registration numbers USNM 158124–158132. Museum specimens are undissected, except where otherwise stated. Dissected specimens are stained with lignin pink and mounted on slides in Euparal. Undissected specimens are preserved in 80% alcohol.

Conchoecia fowleri sp. nov.
(Figs 10–17, 18A–J, 19A–I)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69–70 (in part).—Fowler, 1909 : 249–251 (in part), ? not pl. 23, figs 217 (? = *C. arcuata* Deevey, 1978), 206, 208–210, 212, 214, 216, 218, 220, 222, 224 (= ?), pl. 24, figs 205 (= *C. teretivalvata* Iles, 1953), 207 (= *C. subinflata* sp. nov.), 211, 213, 221, 223 (? = *C. pusilla* Müller, 1906), 215 (= ?), 219 (= *C. teretivalvata* Iles, 1953).
Conchoecia rotundata Müller, 1890, forms 1, 5, 9. Angel & Fasham, 1975 : 737 (distribution).—Angel, 1977a : 246 (vertical distribution). Not *Conchoecia rotundata* Müller, 1890.
Conchoecia skogsbergi Iles, 1953. Angel, 1968b : 308, Fig. 8 (vertical distribution).—Deevey, 1968 : 54–55, Figs 20a–d, 21a, d, f–h, 22a.—Angel, 1969 : 518, 539 (vertical distribution).—Deevey, 1974 : 364 (not Fig. 5b, = *C. skogsbergi* Iles, 1953).—Deevey, 1978a : 70. Not *Conchoecia skogsbergi* Iles, 1953.

ETYMOLOGY. Named after Dr G. H. Fowler, one of the first authors to work on planktonic ostracods from the NW Atlantic.

DIAGNOSIS. Lateral carapace outline elongate, rather gently tapered in anterior 2/3 to 3/4; posterior end symmetrically rounded, or slightly upturned. Length = 1·10–1·28 mm. Ventral carapace outline relatively narrow and weakly biconvex, in $\circ$ B = 38%–43% of length; anteroventral part of each valve not sharply pointed in ventral view. LAG usually lies 12%–15% of length behind tip of rostrum.

TYPE MATERIAL. Holotype: dissected $\circ$ (BMNH 1979.695). Paratypes: 2$\circ\circ$, dissected (BM(NH) 1979.696–697); 18$\circ\circ$, 21$\circ\circ$ (BM(NH) 1979.746–755).

TYPE LOCALITY. *Discovery* Station 7711, haul 32; 52°54·7'–52°56·5'N; 20°12·6'–20°7·7'W; depth 605–700 m; date 22 May 1971; time 2249–0049 hr; gear RMT 1.

OTHER MATERIAL EXAMINED. (i) Approximately 2500♂♂, 3500♀♀ and 5000JJ (DC Wormley). (ii) 21♂♂, 20♀♀ *Discovery* Station 7406, haul 44 (SI Washington, USNM 158126). (iii) 4♀♀, 2♂♂ in Fowler's (1908) material of *C. rotundata* (BM(NH) 1910.72.114). (iv) 1♀, *Valdivia* Station 182, in Müller's (1906a) material of *C. rotundata* (ZIZM, Hamburg K-18937; tentative identification). (v) 4♀♀, 4♂♂, *Gauss* Stations 19.10.01d, 12.11.01, 4.9.03, 30.9.03b, in Müller's (1908) material of *C. rotundata* (ZM, Berlin, 26476). (vi). 1♀, 1J, *Dana* Stations 3613–8, 3624–4, in Poulsen's (1973) material of *Metaconchoecia rotundata* (ZM, Copenhagen).

DESCRIPTION OF THE MALE. *Carapace* (Figs 10, 11A–S). In lateral view the ventral margin is almost straight or gently curved and joins the posterior end evenly. The dorsal margin is either straight or in the shape of a very broad V with the apex just behind the second antenna protopodite insertion; it joins the posterior end at a rounded angle. The rostral incisure is usually fairly shallow. In ventral view, the sides of the carapace are only gently curved. The right asymmetric gland opens near the posterodorsal corner. The left gland opens in an anterior position somewhat behind the incisure. There is no surface ornamentation.

Frontal organ (Figs 14F, 18A–J). The shaft does not extend beyond the end of the first antenna. In general, the proximal half of the capitulum is expanded, with a strongly convex ventral margin, and the distal part is slightly tapered or parallel sided. However, it is somewhat variable and may be narrower, parallel sided, with a strong proximal downflexure (Figs 18F, G, I). Stout ventral spines are developed, particularly on the proximal part.

First antenna (Figs. 14D, E). The segmentation is fairly distinct. Segment 2 bears fine lateral spines. The a seta extends back parallel to the limb, except proximally where it loops down and is rather expanded. The b seta is slightly shorter than the d seta and bears 5–11 closely spaced anterior spines, followed by 5–10 more widely spaced spines with 6–12 spines on the posterior side. The d seta has 8–15 anterior spines, followed by 2–6 more widely spaced spines. The e seta armature comprises 24–30 (mean 26·3, 56 observations) spines which lie at an acute angle to the seta and are paired or less commonly staggered.

Second antenna (Figs 14A–C). The protopodite bears a patch of short hairs behind En 1. Ex 1 has a short distal ventral seta and an area of proximal outer hairs. Posteriorly, En 1 bears 3 triangular ridges covered by fine hairs. The processes mamillaris is bulbous with a beak-like extension pointing slightly forwards. The right hook appendage is strongly developed with a long curved distal section and a number of subterminal ridges; the left hook appendage is smaller, with a short straight distal section and no subterminal ridges. The b seta is > twice the length of the a seta, the d seta is slightly shorter than the c seta and the e seta is a short spine. The f seta is rather longer than the g seta and on its anterior side bears 3–11 small spines; 2–3 spines are sometimes visible on the g seta.

Mandible (Figs 16B–E). The coxale cutting edge has a straight anterior section followed by 11–20 (usually 11–16) teeth. The distal list has a large pointed posterior tooth, followed by 18–26 small teeth. The proximal list has a large pointed, posterior tooth, 1–5 very small teeth, a second large tooth followed by 18–26 very small teeth, one of which, near the middle, is larger than the remainder; the inner surface of this list is covered with papillae. The cutting edge of the basale has two spine teeth, the posterior one pointed, the anterior one more rounded and both devoid of spines or hairs; these are followed by six serrated teeth of which the most posterior lacks secondary cusps. The anterior inner tooth is triangular with small serrations. Near the cutting edge of the basale there are two short setae inside the posterior margin, a longer seta on the anterior margin and a long median seta. The basale also has a long distal median seta below the endopodite. Ex 1 bears an outer distal plumose seta and two setae on the inner edge, one longer than the other. On Ex 2 there are three outer distal setae, one long, one of medium length and the other short, and two setae on the inner edge which are similar to those on Ex 1. Ex 3 has three outer setae, two long and claw like and the third short, and four short inner setae.

Maxilla (Fig. 16G). The anterior margin bears three long setae, of which the most proximal is the longest, and a rather shorter seta arising from just inside the margin. The posterior margin has three fairly long setae. The basal seta extends just beyond the end of the limb. There are 5–7 short spines on the bottom of the main segment.

Labrum (Fig. 16A). The hyaline membrane is interrupted by a deep V-shaped notch. On each side of the notch are 11–12 flaccid, inward facing teeth.

Fifth limb (Fig. 16F). Ex 1 bears seven ventral setae, two of these are posterior (distal), two are median and there are three smaller ones at the anterior end; there is also a long distal dorsal seta and a short lateral distal seta. Ex 2 has a medium sized ventral seta and a slightly longer dorsal seta. Ex 3 bears two fairly long claw-like setae and a shorter ventral seta.

Sixth limb (Fig. 14G). Ventrally, segment 1 bears three short posterior (distal) setae, two median setae, one of them short and the other longer and plumose, and two anterior (proximal) setae, one of them plumose. Segment 2 has a minute ventral seta which points out from the limb. Segment 3 has a minute ventral seta and a similar dorsal seta lying parallel to the limb. The terminal setae are fairly short and are armed with hairs only distally.

Seventh limb (Fig. 16I). The terminal segment bears two setae, one about three times the length of the other.

Caudal furca (Fig. 16H). There is an unpaired seta above the smallest claw seta. The claw setae are unusually straight.

Penis (Fig. 14H). The end of the penis is obliquely truncated. The terminal part of the vas deferens, which is narrow and tubular, lies free in a depression at the end of the penis; this depression is bounded posteriorly by a distinct lobe. There are 3–5 transverse muscles.

DESCRIPTION OF THE FEMALE. *Carapace* (Figs 12, 13A–O). The lateral outline has a more strongly rounded posterior end, but is otherwise like that of the male. In ventral view, the sides of the carapace are almost straight or only slightly curved.

Frontal organ (Figs 15E, 19A–I). The shaft extends well beyond the end of the first antenna and is about twice the combined length of segments 1 and 2. The capitulum is not differentiated from the shaft. It is rather expanded proximally and tapers to a narrowly rounded end. The dorsal surface is sometimes slightly concave near the middle; the ventral surface is usually slightly concave distally. In occasional specimens the end is more pointed and downturned.

First antenna (Figs 15C, D). Segment 2 is about twice the length of segment 1 and bears minute scattered lateral spines. The segmentation is fairly distinct. There is no dorsal seta. The a–d setae are almost twice the length of the e seta and are somewhat expanded beyond their basal stalk. The e seta bears 30–37 posterior spines, extending from near the distal end to just above the middle of the seta; the anterior side has 34–45 spines situated rather more proximally. The e seta tapers to a point and is not flattened.

Second antenna (Figs 15A, B). The armature of the protopodite, Ex 1 and En 2 is similar to that of the male, although the protopodite hairs and Ex 1 spines are not always visible. The a seta is about half the length of the b seta and both carry fine hairs. The c (or ?d) seta is minute and often not visible or absent. The f–g setae are rather > half the length of the protopodite and are devoid of armature.

Sixth limb (Fig. 15F). Segment 1 bears a plumose distal dorsal seta, four distal ventral setae, the longer two of which are plumose, two median ventral setae, the longer one plumose, and a plumose proximal ventral seta. Segment 2 has a single ventral seta. Segment 3 has a ventral median seta and a rather longer dorsal median seta. The terminal segment bears three claw setae, the median one is the longest and the dorsal seta is rather longer than the ventral seta.

DIMENSIONS. ♂ Carapace length: 1·10–1·28 mm, mean 1·21 ± 0·02 mm (n = 978). ♀: 1·12–1·28 mm, mean 1·21 ± 0·02 mm (n = 560). See Tables 3 & 4 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. Judging from the carapace outlines illustrated by Deevey (1968: Fig. 20a, b, 21a, d), her small form of *C. skogsbergi* from the W. Atlantic (Deevey, 1968; 1974; 1978a) is, at least in part, *C. fowleri*. However, the length range of Deevey's specimens extends down to 1·00 mm. This is well below the lower size limit of *C. fowleri* and suggests that she included at least one other species of the *skogsbergi* complex with *C. fowleri*.

One of the specimens figured by Fowler (1909 : 124, fig. 215) was identified by Angel, (1977a: Table 5) as *C. rotundata* form 1 (= *C. fowleri*). However, it cannot be *C. fowleri*, and in fact is impossible to assign to any *rotundata* group species, because it combines an elongate lateral outline with a left asymmetric gland which opens very near the tip of the rostrum.

GEOGRAPHICAL DISTRIBUTION. *Atlantic Ocean:* abundant in the E. Atlantic between 18°N, 25°W and 60°N, 20°W, less common at the equator and 11°N, 20°W (Angel & Fasham, 1975; Angel, 1977a; 1979); occasional specimens in *Gauss* samples from between 6°N and 35°S in the E. Atlantic (Table 2); in the W. Atlantic, fairly common around 32°N, 64°W (Deevey, 1968; Angel, 1979); probably present in the SW Atlantic and off Venezuela (Deevey, 1974; 1978a; as *C. skogsbergi). Indian Ocean:* single tentatively identified specimen in one *Valdivia* sample from E. Indian Ocean (Table 1). *Pacific Ocean:* two specimens in *Dana* material from the SW Pacific.

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 400 m–1250 m; at 60°N, 20°W and 53°N, 20°W it is most common between 400 m and 700 m, further south around 18°N, 25°W and 11°N, 20°W it is most abundant at rather greater depths.

Conchoecia fowleri form A
(Figs 11T–Z, 13P–X, 17)

Conchoecia fowleri form 13.—Angel & Fasham, 1975 : 737.

MATERIAL. 26♀♀, 19♂♂, *Discovery* GATE Stations; 92♀♀, 38♂♂, Station 6665; 1♀, 8♂♂, 7089; 7♀♀, 1♂, 7824; 11♀♀, 6♂♂, 7803 (DC Wormley).

DESCRIPTION. This is a larger, deeper living variant of *C. fowleri*. The lateral outline is similar but in ventral view the carapace is broader than that of *C. fowleri* (Figs 11, 13). The male first antenna b, d and e setae, and the longest swimming seta on the female second antenna tend to be relatively longer.

DIMENSIONS. ♂ Carapace length: 1·28–1·40 mm, mean 1·33 ± 0·02 mm (n = 43). ♀: 1·28–1·38 mm, mean 1·32 ± 0·02 mm (n = 40). See Tables 3 & 4 for other morphometric data and Table 9 for left asymmetric gland position.

REMARKS. This form differs only slightly from typical specimens of *C. fowleri* and does not have a sufficiently distinct depth distribution to be regarded as a subspecies. The broad spectrum of length values for specimens taken at depths of 1000–1500 m near the equator, suggests that the two forms are hybridizing here (Fig. 17). Similar apparent hybridization was reported by Angel (1977b) in *C. elegans,* although Angel's forms were separated geographically, rather than by depth.

Conchoecia discoveryi sp. nov.
(Figs 20–22)

Conchoecia rotundata form 6 Angel & Fasham 1975 : 737 (distribution).—Angel, 1979 : 71–72, Figs 60, 61 (vertical distribution).

ETYMOLOGY. Named after RRS *Discovery.*

DIAGNOSIS. Lateral carapace outline gently tapered in anterior 2/3 to 3/4; posterior end usually somewhat upturned. Length = 0·95–1·18 mm. Ventral outline relatively narrow and weakly biconvex, in ♂ B usually <40% of length; anteroventral part of each valve not sharply pointed in ventral view. LAG lies more posteriorly than in other species of

skogsbergi complex, > 15% of length behind tip of rostrum. ♂ A1 e seta only slightly longer than b and d setae and relatively shorter than in other species of *skogsbergi* complex.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.693). Paratypes: 1 dissected ♀ (BM(NH) 1979.694); 14♀♀, 13♂♂ (BM(NH) 1979.785–794).

TYPE LOCALITY. *Discovery* Station 7711, haul 32; 52°54·7′–52°56·5′N, 20°12·6′–20°7·7′W; depth 605–700 m; date 22 May 1971, time 2249–0049 hr; gear RMT 1.

OTHER MATERIAL EXAMINED. (i) Approximately 3800♀♀, 1500♂♂ and 2900JJ (DC, Wormley). (ii) 10♀♀, 10♂♂ from *Discovery* Station 7711, haul 13 (SI, Washington, USNM 158132). (iii) 1J *Dana* Station 3624–7, in Poulsen's (1973) material of *Metaconchoecia rotundata* (ZM, Copenhagen, tentative identification). (iv) 2♀♀, 1♂ in Fowler's (1909) material of *C. rotundata* (BM(NH) 1910.72.116).

SUPPLEMENTARY DESCRIPTION. **Male.** *Carapace* (Fig. 20). The carapace is only slightly tapered in lateral view. *Frontal organ* (Fig. 22B). The capitulum is similar in shape to that of *C. fowleri* but the ventral spines are rather smaller and more numerous. **Female** *Carapace* (Fig. 21). The lateral outline is like that of the male but rather less elongate; in ventral view the carapace is almost parallel sided. *Frontal organ* (Fig. 22H). The capitulum is less strongly tapered than in *C. fowleri* and has a more bluntly rounded end.

DIMENSIONS. ♂ Carapace length: 0·97–1·14 mm, mean 1·05 ±0·02 mm (n = 664). ♀: 0·95–1·18 mm, mean 1·07 ± 0·02 mm (n = 919). See Tables 3 & 4 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. The lateral outline of *C. discoveryi* tends to be slightly less tapered than that of *C. fowleri* and the posterior end is rather more clearly upturned. The carapace is also somewhat shorter. *C. discoveryi* is distinguished from all other species of the *skogsbergi* complex, including *C. fowleri*, by the relatively posterior position of the left asymmetric gland and the relative shortness of the male first antenna e seta.

GEOGRAPHICAL DISTRIBUTION. *Atlantic Ocean:* abundant in the E. Atlantic between 40°N, 20°W and 60°N, 20°W, less common between 40°N, 20°W and the equator (Angel & Fasham, 1975; Angel, 1979); common in the W. Atlantic around 32°N, 64°W (Angel, 1979). *Pacific Ocean:* single tentatively identified juvenile in *Dana* material from the SW Pacific.

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 600 m–1500 m; it is most abundant between 900 m and 1500 m and particularly between 1000 m and 1250 m. At 53°N 20°W the females are most abundant at 1000–1500 m and the males and juveniles at 600–800 m. A similar separation occurs around 32°N 64°W (Angel, 1979).

Conchoecia obtusa sp. nov.
(Figs 23–25)

?*Metaconchoecia rotundata* (Müller, 1890).—James, 1975 : 114–118, p. XXI, figs l, m, pl. XXII, figs a–l.
Conchoecia rotundata form 2, Angel & Fasham, 1975 : 737 (distribution).—Angel, 1977a : 246 (vertical distribution).—Angel, 1979 : 69–70 (vertical distribution).

ETYMOLOGY. L. *obtusus*, blunt: referring to the fact that the lateral carapace outline is not strongly tapered and the anteroventral part of each valve is rounded or bluntly pointed in ventral view.

DIAGNOSIS. Lateral carapace outline usually only slightly tapered in anterior 1/2–2/3. Ventral outline not strong biconvex, in ♂ B > 41% of length; anteroventral part of each valve not sharply pointed in ventral view. LAG lies < 12% of length behind tip of rostrum. ♂ A1 e seta with 23–28 spines. Posterior end gently, usually symmetrically rounded. Length = 0·91–1·06 mm.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.700). Paratypes: 1 dissected ♀ (BM(NH) 1979.701); 41♀♀, 42♂♂ (BM(NH) 1979.726–735).

TYPE LOCALITY. *Discovery* Station 7856, haul 2; 29°58·1′–29°53·6′N, 23°09′–23°1·8′W; depth 405–505 m; date 31 March 1972; time 0910–1110 hr; gear RMT 1.

OTHER MATERIAL EXAMINED. (i) Approximately 1900♀♀, 1400♂♂ and 1650JJ (DC, Wormley). (ii) 20♀♀, 22♂♂, from *Discovery* Station 7856, haul 8 (SI, Washington USNM 158128). (iii) 1♀ *Dana* Station 3583–1, (ZM, Copenhagen).

SUPPLEMENTARY DESCRIPTION.   **Male.** *Second antenna* (Fig. 25D). The left hook appendage is rather more strongly developed than in *C. fowleri* whereas the right hook is less well developed.   **Female.** *Frontal organ* (Fig. 25H). The end of the capitulum is more pointed and downturned than in *C. fowleri* and the distal part of the ventral margin is clearly concave.

DIMENSIONS. ♂ Carapace length: 0·91–1·00 mm, mean 0·96 ± 0·02 mm (n = 626). ♀: 0·91–1·06 mm, mean 0·97 ± 0·04 mm (n = 672). See Tables 3 and 4 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. *C. obtusa* is consistently smaller than *C. fowleri* and has a rather less tapered, more rectangular outline. In the male, the ventral outline is relatively broader. It is distinguished from *C. discoveryi* by the more symmetrically rounded posterior end, the relatively broader ventral outline of the male and the clearly more anterior position of the left asymmetric gland.
    Judging from the carapace length and outline, *C. rotundata* of James (1975) may be this species.

GEOGRAPHICAL DISTRIBUTION. *Atlantic Ocean*: in the E. Atlantic, abundant at 30°N, 23°W, common at 40°N, 20°W, uncommon at 11°N, 20°W and 18°N, 25°W, rare at the equator, 53°N, 20°W and 60°N, 20°W (Angel & Fasham, 1975; Angel, 1979) and uncommon around 44°N, 13°W (Angel, 1977a); in the W. Atlantic, abundant at 33°N, 64°W (Angel, 1979). *Indian Ocean*: possibly occurs in the NE Indian Ocean (as *C. rotundata* of James, 1975). *Pacific Ocean*: single female in *Dana* material from the SW Pacific.

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 100 m–800 m; it is most abundant between 400 m and 700 m.

Conchoecia skogsbergi Iles, 1953
(Figs 18K–P, 19J–O, 26–29)

Conchoecia rotundata Müller, 1890.—Müller, 1906a : 83–84 (in part, long form only), pl. XVII, figs
    25–33 (not figs 23, 24 = *C. teretivalvata* Iles, 1953).—Müller, 1908 : 69, 70 (in part). Müller 1912 : 77
    (long form only).—Skogsberg, 1920 : 649–658, Fig. CXXII (designated type description by
    Iles, 1953).—Hillman, 1967 : 200 (mentioned only).—Hillman, 1968 : 158 (listed).—Hillman,
    1969 : Map 9 (distribution).
Conchoecia rotundata Müller, 1890, form 10, Angel & Fasham, 1975 : 737 (distribution).
Not *Conchoecia rotundata* Müller, 1890.
Conchoecia skogsbergi Iles, 1953.—Leung, 1972 : 31–32.—Leung, 1973 : 10–11.—Deevey, 1974 : 364
    (in part, ♀ > 1·40 mm, ♂ > 1·35 mm only).—Chavtur & Shornikov, 1974 : 286 (mentioned).—
    Deevey 1978b : 54, 55, Fig. 10.
?*Conchoecia skogsbergi* Iles, 1953.—Angel, 1968a : 1–6, figs 1–10.
Not *Conchoecia skogsbergi* Iles, 1953 (= *C. subinflata* sp. nov.).—Angel 1968b (= *C. fowleri* sp.
    nov.).—Deevey 1968 : 54–55, Figs 20a–d, 21a, d, f–h, 22a (= *C. fowleri*).
?*Metaconchoecia skogsbergi* (Iles, 1953).—Poulsen, 1973: 73–74, Fig. 35.—Chavtur, 1976 :
    105–106.—Chavtur 1977a : 30 (listed).—Chavtur. 1977b : 145–146.
Conchoecia (Metaconchoecia) skogsbergi Iles, 1953.—Deevey, 1978b : 54–55, Fig. 10.

DIAGNOSIS. Lateral carapace outline tapered in anterior 2/3–3/4 and relatively higher than in *C. fowleri*, posterior end approximately symmetrically rounded. Ventral outline rather weakly biconvex, in ♂ >42·5% of length. LAG lies 11%–15% of length behind tip of rostrum. Length > 1·30 mm.

TYPE MATERIAL. Holotype: ♂ (NR Stockholm reg. no. 3101). Paratypes: 2♂♂, 4♀♀, 2JJ (NR Stockholm reg. no. 3101). The type material is part of the collection on which Skogsberg (1920 : 657) based the description of *C. rotundata* that was later designated the type description of *C. skogsbergi* by Iles (1953). Neither the holotype nor the paratypes correspond obviously to Skogsberg's (1920 : Figs CXXII, 1 and 2) figured carapaces, which were, however, also from the type locality.

TYPE LOCALITY. Station 64b of the Swedish 'Antarctic' Expedition of 1901–1903: 48°27'S, 42°36'W; depth 2500–0 m, date 23 June 1902.

OTHER MATERIAL EXAMINED. (i) 2♀♀, 1J, S.A.E. Station 70b in Skogsberg's (1920) material of *C. rotundata* (NR, Stockholm, 238). (ii) 36♀♀, 21♂♂ 12JJ in Müller's (1908) *Gauss* material of *C. rotundata* (Table 2 for station details; ZM, Berlin 26467, 26479, BM(NH) 1924.7.19.184–187). (iii) Specimens collected by *Discovery* II: 2♀♀, 2JJ (*Discovery* Station 1773), 1♀ (1775), 3♂♂ (1776), 2♀♀, 4♂♂, 5JJ (1777), 5♀♀, 1♂, 7JJ (1778), 4♀♀, 1♂, 6JJ (1779), 6♀♀, 2♂♂, 5JJ (1781), 6♀♀, 3♂♂, 2JJ (1782), 2♀ (2018), 1♀, 4JJ (2020), 5♀♀, 10♂♂, 18JJ (2026), 3♀♀ (2391), 1♀, 1♂, 1J (2393), 3♀♀, 3JJ (2495), 1♀ (2496), 3♀♀, 3♂♂, 4JJ (2498), 6♀♀, 4♂♂, 1J (2501) (DC, Wormley). (iv) 2♂♂, dissected, *Discovery* Stations 1777, 1781 (BM(NH) 1979.713, 714); 1♀, dissected (BM(NH) 1979.715), 8♀♀, 1♂ (BM(NH) 1979.756–764) from Station 2393; 4♀♀, 1♂ (BM(NH) 1979.825–827) from Station 1779. (v) Specimens collected by RRS *Discovery*: 1♀ (Station 6665, haul 26), 2JJ (haul 28), 15♀♀, 8♂♂, 16JJ (haul 38), 1♂ (Station 8281, haul 35) (DC, Wormley). (vi) 1♀, dissected, from Norwegian Sea, described by Angel (1968a) (BM(NH) 1979.712). (vii) 1♀, dissected, collected below Arctic ice from Fletchers Ice Island (T3) at 85°58'N, mentioned by Leung (1972, 1973) (BM(NH) 1979.711).

SUPPLEMENTARY DESCRIPTION· **Male.** *Carapace* (Figs. 26A–L). The *Valdivia, Gauss* and *Discovery* samples include small, intermediate and large size forms (Table 6, Appendix 1). In ventral view, the anteroventral region of each valve is rather pointed. The surface is usually smooth but a few specimens from *Gauss* Station 12.11.01 have fine longitudinal striations near the ventral margin. *Frontal organ* (Figs. 18K–P). The capitulum is generally similar to that of *C. fowleri* but tends to vary in shape. Intermediate form: the proximal half of the capitulum is rather expanded with a strongly convex ventral margin, the distal half is parallel sided or slightly tapered. Small form: the capitulum is more slender, the proximal part of the ventral margin being less strongly convex. Large form (one specimen): the capitulum is only slightly expanded proximally with a blunt terminal spine. *First antenna* (Fig. 28A, C). The d seta has a number of minute spines on the postero-lateral surface behind the main anterior spines. *Second antenna* (Fig. 28D, E). There are considerably more spines on the anterior surface of the g seta than in *C. fowleri* (Table 5); these extend down onto the distal thin-walled part of the seta. *Mandible*. On the proximal tooth list, the third large tooth, near the middle of the list, is sometimes comparable in size to the second large tooth.
Female. *Carapace* (Fig. 27). There are three size forms corresponding to those of the male. The lateral outline is similar to the male but is rather variable; in particular, the relative height varies and the ventral margin ranges from being slightly concave in smaller specimens to slightly convex in larger specimens. *Frontal organ* (Fig. 19J–O, 28H). The capitulum outline is variable. In the small and intermediate forms it is similar in shape to that of *C. fowleri* but the captilulum of the large form tends to be relatively higher, the ventral margin is more or less concave in the distal half and the end is more pointed and downturned.

DIMENSIONS. See Table 6 for carapace dimensions, Tables 7, 8 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. The S. Atlantic *Discovery* material of *C. skogsbergi* is closely similar to the specimens described by Müller (1908) and Skogsberg (1920) from the same general area. It also compares closely with the female specimen of Leung (1972 : 1973) which was caught in the central Arctic Ocean. The female described by Angel (1968a) from the Norwegian Sea is rather small for *C. skogsbergi* (Table 6) and differs in a number of morphometric characters from typical Southern Hemisphere material. It is therefore placed only tentatively in this species. *Discovery* specimens from deep water in the tropical N. Atlantic are usually somewhat lower and narrower than typical specimens, but are otherwise similar.

The present, rather sparse, *Discovery* material suggests that the three size forms in the S. Atlantic are only partially separated in depth and are not sufficiently different morphologically to be regarded as distinct species or subspecies. However, it is possible that these populations are becoming genetically isolated and undergoing speciation.

C. skogsbergi is consistently larger than other species of the *skogsbergi* complex with the exception of *C. fowleri* form A from which it differs in being relatively higher in lateral view. It is similar in size to *C. abyssalis* but has a different lateral outline and no side branches on the male first antenna a and c setae and the female first antenna a and d setae.

GEOGRAPHICAL DISTRIBUTION. *Southern Ocean*: common as far as 70°S in all sectors (Müller, 1906a; 1908; 1912; Hillman, 1967; 1968; 1969; Deevey, 1978b; this paper). *South Atlantic*: occurs in *Gauss* and *Discovery* material from the SE Atlantic; present in the SW Atlantic (Skogsberg, 1920; Deevey, 1974). *North Atlantic*: rare in E. Atlantic at 11°N, 20°W and 18°N, 25°W (Angel & Fasham, 1975; this paper); Norwegian Sea (Angel, 1968a; this paper, tentative identification). *Pacific Ocean*: Bering and Okhotsk Seas, Kurile-Kamchatka Trench (Chavtur & Shornikov, 1974; Chavtur, 1976; 1977a; 1977b); SW Pacific (Poulsen, 1973; tentative identification). *Arctic Ocean*: 1 female from the central Arctric Ocean (Leung, 1972; 1973; this paper).

VERTICAL DISTRIBUTION. In *Discovery* material from the S. Atlantic, the small size form occurs mainly in the 250–500 m and 500–750 m horizons, the intermediate form in the 500–750 m and 750–1000 m horizons and the large form in the 750–1000 m and 1000–1500 m horizons (Fig. 29). In *Discovery* material from the tropical N. Atlantic *C. skogsbergi* was taken between 1250 and 3600 m. Deevey (1978b) records it from 500–2000 m in the Pacific sector of the Southern Ocean. Angel (1968a) reports *C. skogsbergi* from 600–1000 m in the Norwegian Sea.

Conchoecia wolferi sp. nov.
(Figs 30, 31)

Conchoecia rotundata form 11, Angel & Fasham 1975 : 737 (distribution).

ETYMOLOGY. The name is an anagram of *fowleri* and reflects the close relationship between these two species.

DIAGNOSIS. Lateral carapace outline rather gently tapered in anterior 2/3 to 3/4. Ventral carapace outline not strongly biconvex, in ♂ B usually >42% of length; anteroventral parts of each valve not sharply pointed in ventral view. LAG lies <12·0% of length behind tip of rostrum. ♂ A1 e seta with 24–28 spines. Posterior end symmetrically rounded or somewhat downturned. Length = 1·06–1·26 mm.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.704). Paratypes: 1 dissected ♀ (BM(NH) 1979.705), 21♀♀, 20♂♂ (BM(NH) 1979.805–814).

TYPE LOCALITY. *Discovery* Station 6665, haul 4; 10°32·7'N, 19°57·4'W; depth 400–295 m; date 22 January 1968; time 1559–1731 hr; gear N113 CDB.

OTHER MATERIAL EXAMINED. (i) Approximately 320♀♀, 200♂♂ and 37JJ (DC, Wormley). (ii) 19♀♀, 17♂♂ from *Discovery* Station 6665, haul 8 (SI, Washington, USNM 158127). (iii) 1♀, *Dana* Station 3583–1 in Poulsen's (1973) material of *Metaconchoecia rotundata* (ZM, Copenhagen, tentative identification).

DIMENSIONS. ♂ Carapace length: 1·06–1·20 mm, mean 1·13 ± 0·02 mm (n = 405). ♀: 1·10–1·26 mm, mean 1·17 ± 0·03 mm (n = 521). See Tables 3 and 4 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. This species is similar in shape to *C. fowleri* and *C. discoveryi* but is broader in ventral view with a somewhat downturned, rather than upturned, posterior end, and a more anteriorly situated left asymmetric gland. *C. wolferi* is consistently larger than *C. obtusa,* the lateral outline is relatively more elongate and the posterior end tends to be more downturned.

GEOGRAPHICAL DISTRIBUTION. *Atlantic Ocean*: fairly common around 11°N, 20°W and 18°N, 25°W in E. Atlantic and on the equator. *Pacific Ocean.* single tentatively identified female in *Dana* material from SW Pacific.

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 300–800 m. At 11°N, 20°W it is most abundant betweeen 300 m and 400 m, at 18°N, 25°W it is most abundant at depths of 400 m to 600 m.

Conchoecia acuta sp. nov.
(Figs 32–34)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69, 70 (in part).
Conchoecia rotundata forms 4, 12 Angel & Fasham 1975 : 737 (distribution).—Angel, 1979 : 71, fig. 59 (vertical distribution).

ETYMOLOGY. L. *acutus,* pointed: referring to the rather strongly tapered lateral outline and the sharply pointed shape of the anteroventral region when viewed ventrally.

DIAGNOSIS. Lateral outline relatively higher than in *C. fowleri* and clearly tapered in anterior 2/3 to 3/4. Posterior end approximately symmetrically rounded. Ventral outline weakly biconvex in ♀ (B = 35–46% of length), more strongly biconvex in ♂ (B = 42·5–50% of length); anteroventral part of each valve pointed in ventral view. LAG lies < 11·5% of length behind tip of rostrum. ♂A1 e seta with 20–24 spines. Length = 0·85–1·00 mm. ♂A2 f seta < 38%, g seta < 42%, ♀ A2 LSS < 41%, f–j seta < 20% of length.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.690). Paratypes: 1 dissected ♀ (BM(NH) 1979.691); 1 dissected ♂ (BM(NH) 1979.692); 20♂♂, 24♀♀ (BM(NH) 1979.736–745).

TYPE LOCALITY. *Discovery* Station 7089, haul 19; 17°48′N, 25°22′W; depth 197–112 m; date 15 November 1969; time 1307–1537 hr; gear RMT 1.

OTHER MATERIAL EXAMINED. (i) Approximately 950♀♀, 550♂♂, 350JJ (DC, Wormley). (ii) 16♀♀, 16♂♂ from *Discovery* Station 7856, haul 22 (SI, Washington USNM 158131). (iii) Specimens in Müller's (1908) material of *C. rotundata*: 81♀♀, 29♂♂, 10JJ (*Gauss* Station 19.10.01d); 26♀♀, 13♂♂ (19.10.01c); 10♀♀, 7♂♂ (26.10.01); 1♀, 2♂♂ (5.11.01a); 3♀♀, 2♂♂ (12.11.01); ?1♀ (18.5.03) (ZM, Berlin, 26465, 26474). (iv) 5♀♀, 3♂♂ in Müller's (1906a) material of *C. rotundata* from *Valdivia* Station 26 (ZM, Berlin, 16483, all tentative identifications).

SUPPLEMENTARY DESCRIPTION. **Male.** *Second antenna* (Figs 34D, E). The hook appendages are similar to those of *C. fowleri* but more nearly equal in size. **Female.** *Frontal organ* (Fig. 34H). The capitulum is similar in shape to that of *C. fowleri* but has a rather more pointed and downturned tip.

DIMENSIONS. ♂ Carapace length: 0·85–0·99 mm, mean 0·91 ± 0·04 mm (n = 457). ♀: 0·85–1·01 mm, mean 0·93 ± 0·01 mm (n = 723). See Tables 11 and 12 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. *C. acuta* resembles Müller's (1890, pl. XXVIII, fig. 42) original *C. rotundata* in lateral view but is more elongate and also considerably smaller. Compared with *C. obtusa*, the lateral outline is more tapered and the ventral outline is more convex with the antero-ventral part of each valve being pointed rather than rounded and the rostrum more produced. *C. acuta* is consistently smaller than *C. fowleri* and *C. wolferi* and the left asymmetric gland has a clearly more anterior position than in *C. discoveryi*.

GEOGRAPHICAL DISTRIBUTION. *North Atlantic Ocean*: common in the E. Atlantic between the equator and 30°N, 23°W (Angel & Fasham, 1975; this paper), but its reported occurrence at 40°N, 20°W has not been confirmed; common in the W. Atlantic around 32°N, 64°W (Angel, 1979; this paper). *South Atlantic Ocean*: fairly common in *Gauss* material from 19°S to 35°S in the E. Atlantic. *Indian Ocean*: 1♀ from the SE Indian Ocean in *Gauss* material (tentative identification).

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 50–500 m; it occurs mainly in the top 300 m, particularly between 100 m and 200 m.

Conchoecia aff. *acuta*
(Figs 35, 36)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69, 70 (in part).
Metaconchoecia rotundata (Müller, 1890).—Poulsen, 1973 : 71–72; Figs 34a–j.

MATERIAL EXAMINED. *Broad form. Dana* Stations 3587–6 (1♂), 3611–2 (1♂, 1J), 3613–3 (25♀♀), 3613–8 (3♀♀, 4♂♂), 3613–9 (3♀♀, 2♂♂), 3613–10 (17♀♀, 14♂♂, 5JJ), 3623–2 (1♀, 1♂), 3623–5 (29♀♀, 10♂♂, 4J), 3624–2 (16♀♀, 7♂♂), 3624–3 (2♀♀, 1♂), 3624–4 (8♀♀, 2♂♂), 3624–5 (27♀♀, 11♂♂), 3624–7 (1♀, 2♂♂, 1J), 3624–8 (60♀♀, 20♂♂, 6JJ), 3625–2 (8♀♀, 6♂♂, 6JJ), 3625–5 (75♀♀, 24♂♂, 19JJ) (ZM, Copenhagen). *Narrow form. Dana* Stations 3613–3 (2♀♀), 3613–10 (3♀♀), 3623–2 (1♂), 3623–5 (6♀♀), 3625–2 (2♀♀, 1♂), 3684–2 (1♀), 3687–10 (2♀♀), (ZM, Copenhagen). *Gauss* Stations 26.10.01 (3♀♀), 5.11.01a (7♀♀) (ZM, Berlin 26474).

REMARKS. Poulsen's (1973) *Dana* material of *Metaconchoecia rotundata* from the SW Pacific mainly comprises a form which is close to *C. acuta* but is relatively broader, with females tending to be widest behind the mid-point (Fig. 35C–Q, 36M–DD). There is also a second form resembling *C. acuta* in the *Dana* samples. This form, which is also present in Müller's (1908) *Gauss* material from the S. Atlantic, is consistently narrower than the broad form, clearly so in females, and on averager is narrower than the typical N. Atlantic form of *C. acuta* (Figs 35A, B, 36A–C). In other respects, both the Pacific forms are closely similar to N. Atlantic specimens.

Because they occur together and differ clearly in carpace width, these broad and narrow forms are probably distinct species. However, their relationship to the Atlantic *C. acuta* is unclear.

DIMENSIONS. See Table 10 for carapace dimensions.

Conchoecia australis sp. nov.
(Figs. 37, 38)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69–70 (in part).—Skogsberg 1920 (in part).

ETYMOLOGY. L. *australis*; referring to the southerly distribution of this species.

DIAGNOSIS. Lateral outline clearly tapered in anterior 2/3 to 3/4, posterior end symmetrically rounded. Length = 0·99–1·08 mm. Ventral outline weakly biconvex in ♀ (B usually <46% of length), more strongly biconvex in ♂ (B = 45–54% of length). Anteroventral part of each valve pointed in ventral view. LAG opens <13% of length behind tip of rostrum. Carapace height usually >50% of length, ♂ A2 LSS >60% and ♀ A2 LSS >47·5% of length.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1980.141). Paratypes: 1 dissected, ♀, 3 dissected ♂♂ (BM(NH) 1980.142–145); 4♀♀, 6♂♂ (BM(NH) 1979.775–784).

TYPE LOCALITY. *Discovery* Station 2026; 38°56′S, 00°10·2′E; depth 500–250 m; date 1 April 1937; time 1600 hr; gear N70V.

OTHER MATERIAL EXAMINED. (i) Material collected by *Discovery* II in the S. Atlantic: *Discovery* Station 1774 (2♀♀, 1♂), 1776 (1♀), 1777 (1♀), 2026 (1♀, 5♂♂, 16JJ), 2386 (2♀♀), (DC, Wormley). (ii) 26♀♀, 4♂♂ from *Gauss* Station 18.12.1 in Müller's (1908) material of *C. rotundata* (ZM, Berlin 26468). (iii) 1♀, 1♂ from S.A.E. Stations 65b and 66b in Skogsberg's (1920) material of *C. rotundata* (NR, Stockholm, 236, 237).

SUPPLEMENTARY DESCRIPTION. **Male.** *Second antenna* (Fig. 38D, E). The left hook appendage passes through a rounded angle of 90° rather than being smoothly curved as in *C. fowleri*. There are 9–10 prominent subterminal ridges. **Female.** *Frontal organ* (Fig. 38H). The capitulum has a rather more pointed and downturned end; the distal part of the ventral margin is somewhat concave.

DIMENSIONS. ♂ Carapace length: 0·98–1·06 mm, mean 1·01 ± 0·02 mm (n = 17). ♀: 0·99–1·08 mm, mean 1·00 ± 0·03 mm (n = 35). See Tables 11 and 12 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. On average, *C. australis* has a relatively higher carapace than other species of the *skogsbergi* complex and the longest swimming setae on the second antenna of both sexes are always proportionally longer than in any species except *C. skogsbergi*. The male first antenna b and d seta and the male second antenna f and g setae also tend to be relatively long. *C. australis* is consistently larger than both *C. rotundata* and *C. acuta*.

GEOGRAPHICAL DISTRIBUTION. *South Atlantic*: known from five stations situated between 39°S and 50°S in the SW and SE Atlantic. *Indian Ocean*: one *Gauss* Station in the SW Indian Ocean.

VERTICAL DISTRIBUTION. The overall depth range in *Discovery* material is 250–750 m. It occurs mainly between 500 m and 750 m.

Conchoecia inflata sp. nov.
(Figs 39–42)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69.70 (in part).
Conchoecia rotundata forms 8, 14, Angel & Fasham, 1975 : 737 (distribution).—Angel, 1977*a* : 246 (vertical distribution).—Angel, 1977*b*: Fig. 1 (size distribution).—Angel, 1979 : 72, Fig. 62 (vertical distribution).
?*Metaconchoecia* cf. *rotundata* 8 sensu Angel, Martens, 1978 : 159.—Martens, 1979 : 351 (possible subspecies).

ETYMOLOGY. L. *inflatus*, swollen; referring to the broad swollen carapace.

DIAGNOSIS. Lateral outline clearly tapered in anterior 2/3 to 3/4. Posterior end gently rounded in ♀, weakly rounded to almost straight in ♂. L = 0·96–1·16 mm. ♂ A1 seta with 19–26 spines. LAG lies <11·5% of length behind tip of rostrum. In ventral view carapace broad, B >46% (♀) >50% (♂) of length, biconvex with strongly curved sides in ♂, curved or almost straight sides in ♀.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.698). Paratypes: 1 dissected ♀ (BM(NH) 1979.699); 8♀♀, 10♂♂ (BM(NH) 1979.716–725).

TYPE LOCALITY. *Discovery* Station 6665, haul 24; 10°31·3′N, 19°58′W; depth 1490–1260 m; date 25 February 1968; time 0404–0835 hr; gear N113 CDB.

OTHER MATERIAL EXAMINED. (i) Approximately 1000♀♀, 850♂♂, 1250JJ (DC, Wormley). (ii) 10♀♀, 12♂♂ from *Discovery* Station 7856, haul 15, (SI, Washington, USNM 158129). (iii) 3♀♀,

1J, *Dana* Station 3587–6, in Poulsen's (1973) material of *Metaconchoecia rotundata* (ZM, Copenhagen). (iv) Specimens in Müller's (1908) material of *C. rotundata* (ZM, Berlin 26480): 2♂♂ (*Gauss* Station 19.10.01d), 2♀♀, 4♂ (12.11.01), 5♀♀, 1♂ (4.9.03), 2♀♀ (30.9.03b). (v) 2♀♀, 1♂ *Valdivia* Station 26, in Müller's (1906a) material (ZM, Berlin 26481, tentative identifications).

SUPPLEMENTARY DESCRIPTION. **Male.** *Frontal organ* (Fig. 41B). The capitulum is similar in shape to that of *C. fowleri* but is relatively higher. *Second antenna* (Figs 41D, E). The right hook appendage is only slightly larger than the left hook. *Penis* (Fig. 42). The number of transverse muscles is unusually variable, ranging from two to six. **Female.** *Frontal organ* (Fig. 41H). The capitulum is relatively higher than in *C. fowleri*, the end is pointed and downturned and the ventral margin distally concave.

DIMENSIONS. ♂ Carapace length: 0·99–1·16 mm, mean 1·08 ± 0·02 mm (n = 493). ♀: 0·97–1·16 mm, mean 1·07 ± 0·03 mm (n = 699). See Tables 11 and 12 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. *C. inflata* is comparable in size to Müller's (1890) original *C. rotundata*. The lateral outline is also similar although relatively lower and more elongate. However, as discussed above, the initial description of *C. rotundata* was inadequate and a proper comparison with other species such as *C. inflata* is now impossible. Martens (1979 : 351) records a form similar to *C. inflata*, possibly a subspecies, from the SE Pacific.

The broad ventral outline, which is particularly obvious in the female, distinguishes *C. inflata* from other *skogsbergi* complex species. The very gently curved, almost vertical posterior end is also characteristic.

GEOGRAPHICAL DISTRIBUTION. *North Atlantic Ocean*: in the E. Atlantic, abundant at 30°N, 23°W, fairly uncommon at 11°N, 20°W, 18°N, 25°W and 40°N, 20°W, rare at 53°N, 20°W (Angel & Fasham, 1975; Angel, 1979; this paper) and uncommon at 44°N, 13°W (Angel, 1977a); in the W. Atlantic, uncommon at 32°N, 64°W (Angel, 1979; this paper). *South Atlantic Ocean*: occurs in *Gauss* material from 12°S to 35°S in the E. Atlantic. *Pacific Ocean*: a few specimens in *Dana* material from the SW Pacific; a related form, possibly a subspecies, occurs off the Chilean coast (Martens, 1979).

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 200–1500 m; it occurs mainly between 200 m and 500 m, but is usually rather deeper (500–600 m) at 32°N, 64°W.

Conchoecia rotundata Müller, 1890
(Figs 43, 44)

Conchoecia rotundata Müller, 1890 : 275, pl. XXVIII, figs 41–43, pl. XXIX, fig. 44.—Müller, 1908 : 69–70 (in part).—Deevey, 1968 : 51–54 (in part: ♀ = 0·77–1·00 mm; ♂ = 0·75–0·97 mm), Figs 20e–j, 21b, c, i, j, k (not 21e, too large: ♂ L = 0·97 mm), 22c–e (not b, too large: ♂ L = 0·97 mm).
Not *Conchoecia rotundata* Müller, 1890.—Hillman, 1967 : 200 (= *C. skogsbergi* Iles, 1953).—Hillman, 1968 : 158 (= *C. skogsbergi*).—Hillman, 1969: Map 9 (= *C. skogsbergi*).—Deevey, 1970 : 810 (too large: ♀ = 0·85–1·15 mm, ♂ = 0·85–1·10 mm).—Poulsen, 1973 : 71–72, text-figs 34a–j (= *C.* aff. *acuta*).—Deevey, 1974 : 364, Fig. 5h (in part) (too large: ♀ = 0·87–0·95 mm, ♂ = 0·80–0·85 mm).—Williams, 1975 : 225, 227, text-fig. 8a (= *C. teretivalvata* Iles, 1953).—Deevey, 1978a : 70 (too large: ♂ = 0·90–0·95 mm, 1·10 mm).
Not *Metaconchoecia rotundata* (Müller, 1890).—James, 1975 : 114–118, pl. XXI, figs 1, m, ml, pl. XXII, figs a–l (? = *C. obtusa* sp. nov.).

DIAGNOSIS. Lateral carapace outline clearly tapered in anterior 2/3 to 3/4. Posterior end approximately symmetrically rounded. Ventral outline weakly biconvex in ♀ (B = 35–43% of length), more strongly in ♂ (B = 41–47% of length); anteroventral part of each valve pointed in ventral view. LAG lies < 11% of length behind tip of rostrum. ♂ A1 e seta with only 14–18 spines. Length = 0·70–0·87 mm.

MATERIAL EXAMINED. (i) Approximately 2100♀♀, 3000♂♂, 100JJ (DC, Wormley). (ii) 1♂, 1♀, both dissected, from *Discovery* Station 8271 (BM(NH) 1979.709, 710); 35♀♀, 40♂♂, from *Discovery* Station 8281, haul 31, (BM(NH) 1979.765–774). (iii) 17♀♀, 25♂♂ from *Discovery* Station 8281, haul 2 (SI, Washington, USNM 158124). (iv) Specimens in Müller's (1908) material of *C. rotundata* (ZM, Berlin 13048, 13049): 1♀, 11♂♂ (*Gauss* Station 19.10.01c), 3♂♂ (19.10.01d) 4♀♀ (26.10.01), 1♀ (12.11.01), 1♀, 1♂ (2.5.03, tentative identifications), 1♀ (18.5.03, tentative identification).

SUPPLEMENTARY DESCRIPTION OF FEMALE. *Frontal organ* (Fig. 44H). The shape of the capitulum is rather different from that of *C. fowleri*. The ventral margin is convex proximally, concave distally and the tip is bluntly pointed and downturned. *First antenna* (Figs 44G, I). Many of the more proximal e seta spines, particularly those on the anterior side, lie close to the seta and because of the small size of this species, they are very difficult to see. *Sixth limb.* As described for *C. fowleri* except that the ventral seta on the final segment is slightly longer than the dorsal seta.

DIMENSIONS. ♂ Carapace length: 0·71–0·83 mm, mean 0·78 ± 0·20 mm (n = 454). ♀: 0·73–0·87 mm, mean 0·80 ± 0·02 mm (n = 446). See Tables 11 and 12 for other morphometric data and Table 9 for left asymmetric gland positions.

REMARKS. The *Discovery* material is closely similar to *C. rotundata* of Deevey (1968). However, there are two differences: (i) Deevey's (1968) specimens have a considerably greater size range (see synonymy for size data) and (ii) the larger specimens have more male first antenna e seta spines (20–22) than any of the males described here. These partial discrepancies suggest that Deevey (1968) included another, larger species of the *skogsbergi* complex with *C. rotundata.* The specimens that Deevey (1970; 1974; 1978a) later placed in *C. rotundata* are all, at least in part, too large (see synonymy) to belong in this species.

Müller's (1908) *Gauss* material of *C. rotundata* includes a few specimens from the Indian and Atlantic Oceans which are closely similar to the *Discovery* specimens. Reexamination of Poulsen's (1973) material shows that his *C. rotundata* belongs to a form close to *C. acuta. C. rotundata* of James (1975) may be *C. obtusa.* Hillman's (1967; 1968; 1969) Antarctic *C. rotundata* is presumably *C. skogsbergi* while the *C. rotundata* caught during Continuous Plankton Recorder surveys of the N. Atlantic (Williams, 1975) is now known to be *C. teretivalvata* (Williams, pers. comm. 1976).

C. rotundata is consistently shorter than any other species of the *skogsbergi* complex and also has fewer male first antenna e seta spines. The lateral outline is relatively higher and more tapered than in *C. fowleri, C. discoveryi, C. obtusa, C. skogsbergi* and *C. wolferi,* and in ventral view, the male carapace is more strongly biconvex, with the anteroventral part of each valve being clearly pointed rather than bluntly pointed or rounded. *C. rotundata* is readily distinguished from *C. kyrtophora, C. nasotuberculata* and *C. teretivalvata* by its more elongate lateral outline.

GEOGRAPHICAL DISTRIBUTION. *Altantic Ocean*: abundant at 30°N, 23°W and 32°N, 64°W and rare at 40°N, 20°W (Angel & Fasham, 1975; Angel, 1977a; 1979; Deevey, 1968; this paper); records from 15°N–35°S in W. Atlantic and off coast of Venezuela (Deevey, 1970; 1974; 1978a) are doubtful (see above); a few specimens in *Gauss* material from 19°S to 35°S in E. Atlantic. *Indian Ocean*: three specimens from two *Gauss* stations in E. and S. Central Indian Ocean (Table 2).

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 100–600 m; it is most common between 200 m and 400 m.

Conchoecia subinflata sp. nov.
(Figs 45–47)

Conchoecia rotundata Müller, 1890.—Müller, 1908 : 69, 70 (in part).—Fowler, 1909 : 249–251, Fig. 205 (Stage II in part; not Stage I = *C. teretivalvata* Iles, 1953).

?*Conchoecia rotundata* Müller, 1890.—Müller, 1906*a* : 183, 184 (in part).
Not *Conchoecia rotundata* Müller, 1890.
Conchoecia skogsbergi Iles, 1953 : 264, 265.
Conchoecia rotundata form 3, Angel & Fasham, 1975 : 737 (distribution).—Angel, 1977*a* : 246
  (vertical distribution).—Angel, 1979 : 70, fig. 58 (vertical distribution).

ETYMOLOGY. L. *sub,* somewhat; *inflatus,* swollen: referring to the fact that the carapace is
similar in shape to that of *C. inflata* but is less inflated.

DIAGNOSIS. Lateral outline clearly tapered in anterior 1/2 and 3/4. Posterior end sym-
metrically rounded. Ventral carapace outline only weakly biconvex, sometimes almost
parallel-sided in ♀ (B = 35%–39% of length), fairly strongly biconvex in ♂; anteroventral part
of each valve clearly pointed in ventral view. LAG lies <11% of length behind tip of
rostrum. ♂ A1 e seta with 18–22 spines. Length = 0·95–1·20 mm. ♂ A2 f seta >40%, g seta
>43%, ♀ A2 LSS >41%, f–j setae >20% of length.

TYPE MATERIAL. Holotype: dissected ♂ (BM(NH) 1979.702). Paratypes: 1 dissected ♀
(BM(NH) 1979.703); 44♀♀, 47♂♂, (BM(NH) 1979.815–824).

TYPE LOCALITY. *Discovery* Station 7709, haul 27; 60°8·7′–60°11·0′N, 19°59·9′–19°51·5′W;
depth 500–600 m; date 28 April 1971; time 1751–1951 hr; gear RMT 1.

OTHER MATERIAL EXAMINED. (i) Approximately 3800♀♀, 2400♂♂, 4600JJ (DC, Wormley). (ii)
44♀♀, 47♂♂, *Discovery* Station 7709, haul 23 (SI, Washington, USNM 158130). (iii) 6♀♀, 2♂♂,
5JJ, *William Scoresby* Station 977, in Iles (1953) material of *C. skogsbergi* (DC, Wormley).
(iv) 2♂♂ in Fowler's (1909) material of *C. rotundata,* redetermined by Iles as *C. skogsbergi*
(BM(NH) 1910.72.117). (v) Specimens in Müller's (1908) material of *C. rotundata* (ZM,
Berlin, 26478, 26466): 1♂ (*Gauss* Station 19.10.01c), 16♀♀, 3♂♂ (19.10.01d), 1♀ (5.11.01a),
3♀♀, 3♂♂ (12.11.01), 1♀ (2.5.03, tentative identification). (vi) 16♀♀, 6♂♂, *Valdivia* Station 121d
in Müller's (1906*a*) material of *C. rotundata* (ZM, Berlin 26482; tentative identifications).
(vii) 1♀, *Dana* Station 3587–6, in Poulsen's (1973) material of *M. rotundata* (ZM,
Copenhagen). (viii) 1♂, *Valdivia* Station 182, in Müller's (1906*a*) material (ZIZM Hamburg
K–18937, tentative identification).

SUPPLEMENTARY DESCRIPTION.   **Male.** *Carapace* (Fig. 45). In ventral view the carapace may
be slightly constricted behind the second antenna insertion. **Female.** *Carapace.* In an
occasional variant (Figs. 46U, CC, DD) the posterior half of the carapace is variably inflated,
the inflation being visible only with the animal on its back. *Frontal organ* (Fig. 47H). The
end of the capitulum is pointed and downturned and the distal part of the ventral surface is
concave.

DIMENSIONS. ♂ Carapace length: 0·95–1·20 mm, mean 1·04 ± 0·02 mm (n = 880). ♀:
0·95–1·18 mm, mean 1·05 ± 0·03 mm (n = 1508). See Tables 11 and 12 for other morpho-
metric data and Table 9 for left asymmetric gland positions.

REMARKS. This species has been identified in some of Fowler's (1909) *C. rotundata* material
from the Bay of Biscay and Fowler's (1909: fig. 205) figured 'Stage I' male has a closely
similar lateral outline. On the other hand, the female carapace outline (Fowler, 1909: fig.
215) is quite different and cannot be assigned to any known *skogsbergi* complex species. The
specimens from the Benguela Current which Iles (1953) placed in *C. skogsbergi* have been
reexamined and identified as *C. subinflata.* A single, rather damaged male in Poulsen's
(1973) material of *Metaconchoecia rotundata* may belong to *C. subinflata* although the left
asymmetric gland is much less prominent and situated further back than in typical
specimens.
    C. subinflata is usually longer than *C. acuta* but the size ranges overlap and specimens of
similar size are difficult to separate. *C. subinflata* has a rather less strongly curved posterior
margin but can only be reliably distinguished from *C. acuta* by differences in the relative
lengths of various seta on the second antenna. Compared with *C. obtusa,* this species usually

has a more clearly tapered lateral outline, the posterior end of the male is less strongly curved and the anteroventral region of each valve is pointed in ventral view rather than being bluntly pointed or rounded. In addition, *C. subinflata* always has more male first antenna e seta spines than *C. obtusa* and there are various meristic differences. *C. subinflata* has a relatively lower lateral outline than *C. australis* and differs in a number of meristic characters. It is similar in lateral outline to *C. inflata* but narrower in ventral view, particularly in the female. *C. subinflata* is consistently larger than *C. rotundata* and the lateral outline is less elongate. The left asymmetric gland is situated more anteriorly than in *C. fowleri* and *C. discoveryi*. The lateral outline is less elongate and more tapered than that of *C. wolferi*.

GEOGRAPHICAL DISTRIBUTION. *North Atlantic Ocean*: In the E. Atlantic abundant at 60°N, 20°W and 53°N, 20°W, fairly common at 40°N, 20°W, 11°N, 20°W and on the equator, uncommon at 18°N, 25°W and 30°N, 13°W (Angel & Fasham, 1975; Angel, 1979; this paper) and common at 44°N, 13°W (Angel, 1977a); rare at 32°N, 64°W in the W. Atlantic (Angel 1979; this paper). *South Atlantic*: occurs between 19°S and 35°S in the SE Atlantic in *Valdivia* and *Gauss* material (Tables 1 & 2); off coast of Namibia in *William Scoresby* material. *Indian Ocean*: 1♂ from NE Indian Ocean in *Valdivia* material (Table 1; tentative identification); 1♀ from S. Indian Ocean in *Gauss* material (Table 2; tentative identification). *Pacific Ocean*: 1♀ in *Dana* material from SW Pacific (tentative identification).

VERTICAL DISTRIBUTION. The overall range in the N. Atlantic is 200–900 m. It is most abundant between 200 m and 400 m.

Species relationships within the *rotundata* group

The 19 or 20 species of the *rotundata* group now described fall into three more or less coherent assemblages.

(i) *C. kyrtophora* and *C. nasotuberculata*: the carapace is short and tapered, relatively high and rounded in lateral view with the left asymmetric gland near the tip of the rostrum or just behind the rostrum; viewed ventrally, the carapace is constricted behind the second antenna insertion. These two species are closely related and have frequently been confused but are now known to be quite distinct (Angel, in press). A third species, *C. teretivalvata,* has a similar lateral outline but it lacks the constriction and the shape of the frontal organ capitulum suggests that it may be more closely related to the *skogsbergi* complex.

(ii) *C. arcuata, C. bathyrotundata* Chavtur, 1977 (a possible synonym of *C. arcuata*), *C. isochiera, C. macromma, C. pusilla* and *C. glandulosa*: the ventral margin is arcuate (strongly in *C. isochiera* and *C. arcuata*); except in *C. arcuata*, the right asymmetric gland is displaced some distance down the posterior margin and opens at the end of a triangular process, the left asymmetric gland usually opens in a relatively posterior position, some distance behind the rostrum (particularly in *C. glandulosa, C. macromma* and, to a lesser extent, *C. arcuata*). Within this assemblage, *C. arcuata* and *C. isochiera* are probably closely related while *C. glandulosa*, a large species with a distinctive outline, is probably rather distantly related to the remaining species.

(iii) The ten species of the *skogsbergi* complex: viewed laterally, the carapace is variably tapered, more elongate than in assemblage (i) species and differing from assemblage (ii) species in having an almost straight or slightly curved ventral margin; the right asymmetric gland always opens near the posterior dorsal corner; the left asymmetric gland position is rather variable but it generally opens near the tip of the rostrum. The rare deep water species *C. abyssalis*, the only described member of the *rotundata* group not represented in the *Discovery* collections, may also belong to the *skogsbergi* complex and *C. teretivalvata* should possibly be placed here rather than in assemblage (i). Within the complex there are two groupings. The first comprises *C. fowleri, C. discoveryi, C. obtusa, C. skogsbergi* and *C.*

wolferi in which the carapace is more elongate in lateral view, less strongly biconvex in ventral view with the anteroventral part of each valve being bluntly pointed. The second group comprises *C. acuta, C. australis, C. inflata, C. rotundata* and *C. subinflata* all of which have relatively shorter, more clearly tapered lateral outlines, more strongly biconvex ventral outlines with the anteroventral part of each valve clearly pointed.

Acknowledgements

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Appendix 1

Just before this paper was submitted, I received from the E.M.-Arndt-Universität, Griefswald a collection of 520 *Valdivia* specimens (reg. no. II 25095), determined by G. W. Müller as *C. rotundata*. These specimens have been re-identified and the new identifications are listed below. The station positions are from Müller (1906a).

Eastern Atlantic Ocean

Station	Position	Species present
32 nr. 43	24°43′N, 17°1′W	*C. brachyaskos* 1♀; *C. inflata* 5♀♀; *C. subinflata* 3♀♀; *C. teretivalvata* 35♀♀, 7♂♂, 5JJ; *C. rotundata* group species indeterminate, 65 specimens; *Conchoecia* species indeterminate, 7 specimens.
41	8°58′N, 16°27′W	*C. inflata*, 7♀♀, 1♂, 1J; *C. macrochiera* 1J; *C. nasotuberculata* 2♀♀; *C. procera* 2♀♀; *C. spinirostris* 4♀♀; *C.* cf. *subinflata* 6♀♀, 3♂♂, 4JJ; *C. rotundata* group species indeterminate, 28 specimens.
49	0°20′N, 6°45′W	*C. acuta* 3♀♀; *C. discoveryi* 1♂; *C. elegans* 1♀; *C. fowleri* 12♀♀, 1♂, 1J; *C. inflata* 14♀♀, 3♂♂, 2JJ; *C. procera* 2♀♀; *C. spinirotris* 2♀♀; *C. subinflata* 13♀♀, 3♂♂, 1J; *C. teretivalvata* 4♀♀, 3♂♂; *C. rotundata* group species indeterminate 7♀♀, 3♂♂, 4JJ; *Conchoecia* species indeterminate 7♀♀.
66	3°55′S, 7°48′E	*C.* cf. *inflata* 4♀♀, 1♂; *C.* aff. *teretivalvata* 1♀.

Southern Ocean

Station	Position	Species present
132	55°20′S, 5°15′E	*C. skogsbergi* 2♀♀ (length = 1·645 mm) 2♂♂ (length = 1·748, 1·773 mm).
135	56°30′S, 14°29′E	*C. skogsbergi* 12♀♀, 5♂♂, 1J. There are three size forms. ♀♀: 1·388, 1·439–1·491, 1·645–1·722 mm. ♂♂: 1·413, 1·491–1·542, 1·645–1·670 mm.
136	55°58′S, 16°14′E	*C. skogsbergi* 1♀ (length = 1·456 mm) 2♂♂ (length = 1·413 mm).
139	55°1′S, 21°34′E	*C. skogsbergi* 7♀♀, 10♂♂. There are two size forms. ♀♀: 1·413, 1·619–1·696 mm. ♂♂: 1·413–1·439 mm, 1·619–1·748 mm.
142	55°27′S, 28°58′E	*C. skogsbergi* 4♀♀, 6♂♂, 1J. There are two size forms. ♀♀: 1·362–1·439, 1·568 mm. ♂♂: 1·413–1·439, 1·568 mm.

Indian Ocean

Station	Position	Species present
217	4°56′N, 78°15′E	*C. hyalophyllum* 1J; *C. lophura* 2JJ; *C.* aff. *subinflata* 27♀♀, 23♂♂, 4JJ; *C. teretivalvata* 27♀♀, 2♂♂, 1J; *C. rotundata* group species indeterminate 2♀♀.
230	2°43′S, 61°12′E	*C. inflata* smaller form 48♀♀ (length = 0·951–1·079 mm), 36♂♂ (length = 0·951–1·002 mm), 3JJ; *C. inflata* larger form 4♀♀ (length = 1·113–1·208 mm), 5♂♂ (length = 1·081–1·156 mm); *C. macromma* 1♀, 2♂♂; *C. procera* 1♀; *C. rotundata* group species indeterminate 2♀♀, 7JJ.
268	9°6′N, 53°41′E	*C.* cf. *subinflata* 1♀; *C. rotundata* group species indeterminate 3♀♀, 1♂, 4JJ.

Table 1 Species identified in material collected by the *Valdivia* during the Deutsche Tiefsee-Expedition and determined by G. W. Müller as *C. rotundata*.

Station	Position	Species present
		North Atlantic Ocean
26	31°59′N, 15°5′W	*C.* cf. *acuta* 5♀ 3♂, *C.* cf. *inflata* 2♀, 1♂.
		South Atlantic Ocean
88	31°0′S, 8°0′E	*C. kyrtophora* 1♀; *C. teretivalvata* 36♀, 6♂, 5J; *rotundata* group indeterminate 2♀.
90	33°20′S, 15°58′E	*C. teretivalvata* 8♀, 4♂, 6J; *rotundata* group indeterminate 1♀.
118	40°31′S, 15°6′E	*C. teretivalvata* 1♀.
121d	43°51′S, 13°6′E	*C.* aff. *subinflata* 16♀, 6♂.
		Indian Ocean
174	27°58′S, 91°40′E	16 indeterminate specimens
182	10°8′S, 97°14′E	*C.* cf. *subinflata* 1♂, *C.* cf. *fowleri* 1♀; indeterminate 1J.

Specimens from Stations 118 and 182 are in the ZIZM, Hamburg (reg. nos K–18937, 18989), other specimens are in the ZM, Berlin (reg. nos 13335, 26481–26485). Station positions are from Müller (1906a).
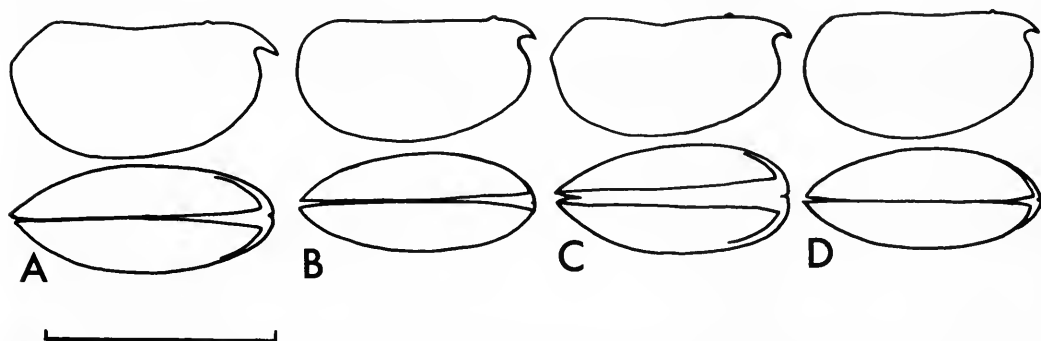

Fig. 1 Lateral and ventral carapace outlines: A, *Conchoecia macromma* ♀, Station 7089 haul 9; B, *C. arcuata* ♀, 7711 haul 47; C, *C. macromma* ♂, 7089 haul 9; D, *C. arcuata* ♂, 7709 haul 12. Scale 1·0 mm.

Table 2 Species identified in material collected by the *Gauss* during the Deutsche Südpolar-Expedition and determined by G. W. Müller as *C. rotundata*.

Station	Position	Species present
		North Atlantic Ocean
30.9.03b	6°N, 22°W	*C. fowleri* 1♀, 1♂; *C. inflata* 2♀.
1.10.03	6°N, 22°W	*rotundata* group indeterminate 1♂.
		South Atlantic Ocean
19.10.01c	19°3′S, 20°W	*C. acuta* 26♀, 13♂, 3J; *C. rotundata* 1♀, 11♂; *C. subinflata* 1♂; *C. procera* 1♀.
19.10.01d	19°3′S, 20°W	*C. acuta* 81♀, 29♂, 10J; *C. fowleri* 1♀ 2♂; *C. inflata* 2♂; *C. rotundata* 3♂; *C. subinflata* 16♀, 3♂.
26.10.01	27°3′S, 16°59′W	*C. acuta* 10♀, 7♂, 1J; *C. aff. acuta* 3♀; *C. rotundata* 4♂; *C. teretivalvata* 1♀.
5.11.01a	32°5′S, 8°30′W	*C. acuta* 1♀, 2♂; *C. aff. acuta* 7♀; *C. subinflata* 1♀; *C. teretivalvata* 4♀; *C. spinirostris* 1♂.
12.11.01	35°11′S, 2°43′E	*C. acuta* 3♀, 2♂; *C. arcuata* 1♀; *C. fowleri* 1♂, *C. inflata* 2♀, 4♂; *C. rotundata* 1♀; *C. subinflata* 3♀, 3♂; *C. skogsbergi* 5♀, 3J; *C. teretivalvata* 124♀, 34♂, 8J; *C. nasotuberculata* 2♀.
10.8.03	30°S, 11°E	*C. teretivalvata* 1♀.
13.8.03	29°8′S, 8°49′E	*C. teretivalvata* 4♀, 6♂, 1J.
19.8.03	27°30′S, 3°7′E	*C. teretivalvata* 22♀, 16♂, 10J.
4.9.03	12°11′S, 6°14′W	*C. fowleri* 2♀; *C. inflata* 5♀, 1♂; *C. pseudoparthenoda* 1♀.
		Indian Ocean
18.12.01	43°41′S, 36°22′E	*C. skogsbergi* 9♀, 3♂, 2J; *C. australis* 26♀, 4♂.
2.5.03	32°33′S, 73°79′E	*C. cf. rotundata* 1♀, 1♂; *C. cf. rotundata* 1♀.
18.5.03	26°54′S, 50°17′E	*C. cf. acuta* 1♀; *C. cf. rotundata* 1♀; indeterminate 1J.
		Southern Ocean
13.2.02	61°58′S, 95°8′E	*C. arcuata* 1♀; *C. skogsbergi* 3♀, 2♂, 1J.
6.3.03	65°S, 85°E	*C. skogsbergi* 1♀, 2♂.
10.3.03	64°29′S, 85°36′E	*C. skogsbergi* 10♀, 5♂, 4J; indeterminate 1♂.
27.3.03	65°S, 80°E	*C. arcuata* 2♀, 1♂; *C. skogsbergi* 7♀, 7♂, 1J.
3.4.03	65°S, 80°E	*C. arcuata* 1♀; *C. skogsbergi* 1♀, 2♂, 1J.

Specimens from Station 3.4.03 are in the BM(NH) (reg. no. 1924.7.19.184–188), other specimens are in the ZM, Berlin (reg. nos 13048–13050, 26465–26485). Station positions are from Müller (1908). The name *C. rotundata* is used in the sense of Deevey (1968).

Table 3   Male morphometric characters.

	C. fowleri sp. n.	*C. fowleri* form A	*C. discoveryi* sp. n.	*C. wolferi* sp. n.	*C. obtusa* sp. n.
N	42	9	20	22	21
H	44·8 ± 1·0	44·1 ± 1·3	45·1 ± 0·9	43·9 ± 1·0	45·6 ± 1·0
B	41·0 ± 1·3	45·5 ± 2·2	39·4 ± 0·9	44·4 ± 1·6	44·3 ± 1·7
F.O.: shaft	28·9 ± 0·6	28·1 ± 0·6	27·1 ± 0·6	29·3 ± 0·7	28·7 ± 0·7
capitulum	11·8 ± 0·3	10·7 ± 0·5	11·0 ± 0·4	12·1 ± 0·8	12·4 ± 0·5
total	40·6 ± 0·6	38·7 ± 0·7	38·2 ± 0·7	41·5 ± 1·0	41·1 ± 0·9
A1: seg. 1	15·0 ± 0·4	14·9 ± 0·6	15·6 ± 0·4	15·5 ± 0·6	15·3 ± 0·3
seg. 2	18·0 ± 0·3	17·7 ± 0·3	15·7 ± 0·3	18·4 ± 0·4	18·3 ± 0·4
total	33·1 ± 0·5	32·6 ± 0·8	31·4 ± 0·6	33·9 ± 0·7	33·6 ± 0·4
a seta	31·0 ± 1·9	31·9 ± 2·8	27·2 ± 2·0	31·0 ± 2·5	34·1 ± 2·3
b seta	43·7 ± 0·7	45·0 ± 0·8	39·5 ± 0·8	45·0 ± 1·2	44·2 ± 0·9
c seta	4·2 ± 0·5	4·7 ± 0·5	4·1 ± 0·6	4·2 ± 0·4	4·5 ± 0·6
d seta	45·8 ± 1·0	47·3 ± 0·7	40·9 ± 0·9	46·5 ± 0·9	46·2 ± 1·0
e seta	53·0 ± 0·7	55·6 ± 0·8	42·1 ± 0·7	57·6 ± 1·3	55·9 ± 0·9
A2: protop.	47·7 ± 0·8	46·7 ± 0·8	46·9 ± 0·7	49·7 ± 0·9	49·1 ± 1·2
Ex. 1	21·2 ± 0·4	21·9 ± 0·2	21·9 ± 0·6	21·8 ± 0·3	22·1 ± 0·5
Ex. 2–8	8·2 ± 0·2	7·8 ± 0·3	8·5 ± 0·3	8·7 ± 0·2	8·5 ± 0·6
LSS	53·7 ± 1·1	54·7 ± 2·0	53·8 ± 1·1	52·5 ± 1·1	52·2 ± 1·8
f seta	39·4 ± 1·0	39·1 ± 0·8	34·9 ± 1·0	37·0 ± 1·0	38·9 ± 1·2
g seta	41·7 ± 0·6	40·7 ± 1·0	37·7 ± 0·6	39·9 ± 1·4	43·0 ± 1·5
h–j setae	15·8 ± 1·3	14·7 ± 1·6	15·6 ± 1·4	15·0 ± 1·5	16·0 ± 1·3

All measurements are expressed as percentages of the carapace length. The measurements are mean values, followed by standard deviations. N = number of observations.

Table 4   Female morphometric characters.

	C. fowleri sp. n.	*C. fowleri* form A	*C. discoveryi* sp. n.	*C. wolferi* sp. n.	*C. obtusa* sp. n.
N	46	10	20	21	23
H	46·7 ± 1·4	45·6 ± 0·7	47·8 ± 1·2	44·8 ± 2·3	46·7 ± 1·1
B	37·5 ± 1·1	40·5 ± 2·8	37·8 ± 1·6	38·6 ± 1·9	39·5 ± 1·7
F.O.: shaft	24·5 ± 1·2	24·6 ± 0·9	25·2 ± 0·9	25·7 ± 0·6	26·4 ± 0·5
capitulum	9·9 ± 0·9	10·4 ± 0·4	10·8 ± 0·4	11·2 ± 0·5	11·7 ± 0·5
total	34·6 ± 0·9	35·1 ± 0·7	35·9 ± 0·9	36·8 ± 0·8	38·1 ± 0·9
A1: segs 1 + 2	11·8 ± 0·4	11·8 ± 1·0	12·8 ± 0·7	13·0 ± 0·4	12·8 ± 0·6
a–d setae	16·5 ± 1·5	15·0 ± 1·4	17·5 ± 1·9	17·3 ± 1·3	17·6 ± 1·8
e setae	33·7 ± 0·8	33·4 ± 1·5	33·5 ± 1·9	34·9 ± 0·9	36·6 ± 1·2
A2: protop.	43·1 ± 0·6	42·0 ± 0·9	42·3 ± 0·7	45·4 ± 0·7	45·2 ± 0·8
Ex. 1	20·2 ± 0·4	21·4 ± 0·4	21·0 ± 0·4	20·3 ± 0·5	21·2 ± 0·4
Ex. 2–8	7·7 ± 0·2	7·5 ± 0·3	8·4 ± 0·4	8·1 ± 0·2	8·4 ± 0·4
LSS	42·1 ± 0·5	44·8 ± 0·8	45·8 ± 1·0	41·3 ± 0·8	43·4 ± 1·1
f–j setae	22·2 ± 1·1	23·1 ± 1·4	24·7 ± 1·5	22·0 ± 0·5	25·1 ± 1·7

All measurements are expressed as percentages of the carapace length. The measurements are mean values, followed by standard deviations. N = number of observations.

Table 5 Morphological details of five *skogsbergi* complex species.

	fowleri sp. n.	*discoveryi* sp. n.	*obtusa* sp. n.	*skogsbergi* SF	IF	LF	*wolferi* sp. n.
♂A1:							
b seta } ant. side	5–11:5–10	6–11:8	7–9:4–10	7–9:4–9	9–11:6–9	12:11	8–14:3–9
spines } post. side	6–12	7	3–6	10–12	14–18	14	4–8
d seta } ant. side	8–15:2–6	9–16:3–5	10–15:3–4	14–16:3–5	15–20:3–8	18–19:10	11–16:4–5
spines } post. side	–	–	–	6–7	5–8	8	–
e seta spines	24–30	20–25	23–28	26–28	28–31	30	24–28
♂A2:							
f seta spines	3–11	5–9	4–5	6–11	11–14	17	3–4
g seta spines	2–3	3–6	2–3	15–29	20–32	21–22	2–5
Penis muscle	3–5	2–5	4	3	4	5	4
♀A1:							
e seta } ant. side	34–45	30–40	30–42	41–62	44–61	57–62	37–47
spines } post. side	30–37	25–37	37–41	40–56	40–65	50–61	37–44
Mandibular teeth:							
cutting edge	11–20	12–14	10–13	14–15	13	11–14	13–16
distal list	18–26	17–23	16–24	19–23	22–24	21–26	19–22
proximal list	18–26	17	17–20	24–25	24–27	22–23	14–18

The first range of numbers given for the ♂A1 b and d setae spines refers to the more proximal, closely spaced spines, the second range is for the more distal, widely spaced spines. Note that the ♂A1 f and g setae spines and some of the spines on the ♀A1 e seta and the ♂A1 b and d setae can be seen only by carefully examining these setae under high magnification. SF = small form; IF = intermediate form; LF = large form.

Table 6 Carapace length data (in mm) for *Conchoecia skogsbergi*.

Material	Provenance of material	N	Females Range	Mean ± SD	N	Males Range	Mean ± SD
Types	S. Atlantic	4	1·43–1·58	1·52	2	1·49–1·54	1·51
Gauss SF	Antarctic	19	1·34–1·45	1·38 ± 0·03	12	1·31–1·37	1·34 ± 0·02
Gauss IF	Antarctic	3	1·52–1·55	1·54	1	–	1·41
Gauss LF	Antarctic	2	1·60–1·61	1·60	2	–	1·66
Discovery SF	S. Atlantic	31	1·34–1·42	1·39 ± 0·02	14	1·32–1·42	1·35 ± 0·03
Discovery IF	S. Atlantic	13	1·46–1·52	1·47 ± 0·02	10	1·46–1·52	1·49 ± 0·02
Discovery LF	S. Atlantic	12	1·56–1·64	1·54 ± 0·07	1	–	1·66
Gauss SF	S.W. Indian	8	1·40–1·46	1·43 ± 0·02	–	–	–
Gauss IF	S.W. Indian	1	–	1·52	3	1·43–1·46	1·44
Gauss SF	S.E. Atlantic	2	1·46–1·47	1·46	–	–	–
Gauss IF	S.E. Atlantic	3	1·51–1·55	1·52	–	–	–
Discovery	N.E. Atlantic	11	1·46–1·54	1·50 ± 0·03	7	1·52–1·62	1·57 ± 0·03
Angel (1968*a*)	Norwegian Sea	1	–	1·34	–	–	–
Leung (1972, 1973)	Arctic	1	–	1·51	–	–	–
Total		111	1·34–1·64	1·45	52	1·31–1·62	1·44

N = number of observations; SD = standard deviation; SF = small form; IF = intermediate form; LF = large form. The *Gauss* specimens are from Müller's (1908) material of *C. rotundata*.

Table 7 *Conchoecia skogsbergi*: female morphometric characters for the three forms in *Discovery* material from the S. Atlantic.

	Small form	Intermediate form	Large form
N	10	8	10
H	50·1 ± 1·0	50·8 ± 0·7	50·6 ± 0·8
B	42·0 ± 1·2	41·0 ± 1·2	39·4 ± 1·6
F.O.: shaft	24·1 ± 0·5	24·3 ± 0·3	23·8 ± 0·8
capitulum	10·8 ± 0·8	11·0 ± 0·5	10·4 ± 0·4
total	34·9 ± 1·0	35·2 ± 0·5	34·1 ± 1·0
A1: segs 1 + 2	11·9 ± 0·8	12·0 ± 0·9	12·2 ± 1·0
a–d setae	14·6 ± 1·7	15·5 ± 1·5	15·5 ± 2·0
e seta	36·7 ± 1·2	36·7 ± 1·3	36·3 ± 1·2
A2: protop.	45·1 ± 0·6	45·2 ± 1·1	44·3 ± 0·9
Ex. 1	22·6 ± 0·6	22·6 ± 0·4	22·3 ± 0·6
Ex. 2–8	8·0 ± 0·3	7·6 ± 0·4	7·6 ± 0·2
LSS	48·6 ± 1·6	46·9 ± 0·8	47·2 ± 0·8
f–j setae	22·0 ± 2·1	22·9 ± 1·6	23·3 ± 1·8

All measurements are expressed as percentages of carapace length. The measurements are mean values, followed by standard deviation. N = number of observations.

Table 8 *Conchoecia skogsbergi:* male morphometric characters for the three forms in *Discovery* material from the S. Atlantic.

	Small form	Intermediate form	Large form
N	14	10	1
H	49·5 ± 0·6	49·1 ± 1·1	50·0
B	44·9 ± 1·5	43·8 ± 0·8	–
F.O.: shaft	30·2 ± 0·5	30·8 ± 0·8	33·8
capitulum	12·1 ± 0·5	12·3 ± 0·3	11·9
total	42·4 ± 1·1	43·1 ± 1·0	45·7
A1: seg. 1	15·0 ± 0·3	14·6 ± 0·4	14·7
seg. 2	20·4 ± 0·3	19·8 ± 0·5	20·9
total	35·4 ± 0·3	34·6 ± 0·8	34·0
a seta	22·0 ± 1·5	28·1 ± 2·9	21·8
b seta	46·7 ± 1·3	48·4 ± 1·0	49·7
c seta	3·2 ± 0·2	3·8 ± 0·5	3·4
d seta	48·0 ± 0·9	50·6 ± 1·2	51·6
e seta	57·1 ± 1·1	62·1 ± 0·9	62·1
A2: protop.	49·5 ± 0·5	49·9 ± 0·7	48·9
Ex. 1	23·1 ± 1·1	23·2 ± 0·5	28·1
Ex. 2–8	7·8 ± 0·4	8·1 ± 0·2	7·0
LSS	58·9 ± 1·7	56·5 ± 1·2	56·6
f seta	43·8 ± 0·6	40·5 ± 0·9	42·7
g seta	48·3 ± 1·1	44·6 ± 1·7	47·9
h–j seta	12·8 ± 2·2	15·0 ± 3·0	14·4

All measurement are expressed as percentages of carapace length. The measurements are mean values, followed by standard deviations. N = number of observations.

Table 9 Left asymmetric gland positions.

Species	Provenance of material	Females N	Mean ± SD	Males N	Mean ± SD
C. fowleri sp. nov.	53°N, 20°W	20	13·6 ± 0·5	20	13·8 ± 0·7
C. fowleri sp. nov.	11°N, 20°W	16	13·4 ± 1·0	17	12·7 ± 0·7
C. fowleri form A	11°N, 20°W	13	14·2 ± 0·8	13	13·9 ± 0·6
C. discoveryi sp. nov.	53°N, 20°W	21	17·7 ± 1·0	20	17·9 ± 0·7
C. obtusa sp. nov.	40°N, 20°W	20	12·2 ± 0·9	20	11·7 ± 0·5
C. skogsbergi types	S. Atlantic	3	12·2	1	11·9
C. skogsbergi SF	S. Atlantic	23	13·7 ± 0·7	11	13·3 ± 0·4
C. skogsbergi IF	S. Atlantic	9	14·1 ± 0·7	7	12·9 ± 0·4
C. skogsbergi LF	S. Atlantic	7	13·0 ± 0·5	–	–
C. skogsbergi	11°N, 20°W	5	12·2	4	11·9
C. skogsbergi	Arctic (86°N)	1	12·6	–	–
C. wolferi sp. nov.	11°N, 20°W	47	11·0 ± 0·6	42	10·7 ± 0·5
C. acuta sp. nov.	18°N, 25°W	22	9·8 ± 0·7	20	10·5 ± 0·5
C. australis sp. nov.	39°S, 00°E	10	12·7 ± 1·9	9	10·7 ± 0·7
C. inflata sp. nov.	30°N, 23°W	20	10·8 ± 0·5	20	10·7 ± 0·5
C. rotundata	30°N, 23°W	21	8·9 ± 0·7	22	9·3 ± 0·6
C. subinflata sp. nov.	60°N, 20°W	20	9·7 ± 0·7	20	9·7 ± 0·7

The gland positions are expressed as percentages of the carapace length behind the tip of the rostrum. The Arctic specimen of *C. skogsbergi* is that of Leung (1972. 1973), SF = small form; IF = intermediate form; LF = large form; N = number of observations; SD = standard deviation.

Table 10 Carapace length (L) height (H) and breadth (B) data for the narrow and broad forms of *C.* aff. *acuta.*

Females

	Narrow form			Narrow form (*Gauss* material)			Broad form		
N		Range	Mean ± SD	N	Range	Mean ± SD	N	Range	Mean ± SD
L 18		0·84–0·93	0·89 ± 0·03	8	0·90–0·96	0·93 ± 0·02	174	0·87–0·97	0·93 ± 0·02
H 15		43·1–50·9	47·49 ± 2·08	7	45·90–49·18	47·52 ± 1·14	31	45·90–50·00	48·17 ± 1·13
B 15		32·79–44·83	38·93 ± 3·04	4	33·33–40·98	35·85	31	41·37–54·39	45·94 ± 3·31

Males

	Narrow form		Broad form		
N		Range	N	Range	Mean ± SD
L 2		0·85–0·94	80	0·85–0·95	0·90 ± 0·02
H 2		44·64–51·61	22	42·37–48·28	46·02 ± 1·40
B 2		44·64–47·90	22	47·32–57·89	51·46 ± 2·65

Height and breadth are expressed as percentages of the carapace length. N = number of observations; SD = standard deviation. Except where indicated, the specimens are from Poulsen's (1973) *Dana* material of *Metaconchoecia rotundata*. The *Gauss* material is from Müller's (1908) material of *C. rotundata.*

Table 11   Male morphometric characters.

	C. acuta sp. n.	C. australis sp. n.	C. inflata sp. n.	C. rotundata	C. subinflata sp. n.
N	41	9	30	20	42
H	46·2 ± 1·3	50·6 ± 1·1	48·0 ± 1·0	47·7 ± 1·4	46·5 ± 0·9
B	48·0 ± 2·6	48·9	53·0 ± 2·1	44·5 ± 2·0	46·4 ± 2·2
F.O.: shaft	30·5 ± 0·6	33·1 ± 0·6	29·3 ± 0·4	29·8 ± 0·74	30·1 ± 0·6
capitulum	12·5 ± 0·5	12·4 ± 0·4	13·4 ± 0·2	12·1 ± 0·6	12·2 ± 0·5
total	42·9 ± 0·8	45·5 ± 0·6	42·7 ± 0·7	41·9 ± 0·2	42·3 ± 1·0
A1: seg 1	15·9 ± 0·4	16·1 ± 1·0	15·5 ± 0·4	15·1 ± 0·2	14·8 ± 0·3
seg 2	18·8 ± 0·4	20·3 ± 0·4	18·5 ± 0·4	18·6 ± 0·6	19·0 ± 0·8
total	34·8 ± 0·5	36·6 ± 1·0	34·0 ± 0·7	33·8 ± 0·8	34·0 ± 0·9
a seta	25·1 ± 2·5	22·4 ± 3·8	26·8 ± 2·1	27·6 ± 2·2	25·2 ± 1·6
b seta	43·9 ± 1·1	49·5 ± 1·0	46·1 ± 0·9	43·8 ± 1·0	44·1 ± 0·8
c seta	3·3 ± 0·4	3·1 ± 0·4	3·5 ± 0·7	4·0 ± 0·4	4·0 ± 0·4
d seta	45·6 ± 0·9	50·9 ± 1·3	48·2 ± 1·0	45·4 ± 0·9	46·1 ± 0·8
e seta	56·5 ± 0·9	58·7 ± 1·1	60·0 ± 1·2	52·4 ± 1·4	54·3 ± 1·0
A2: protop.	51·7 ± 0·8	53·1 ± 1·6	50·8 ± 0·8	49·4 ± 0·8	49·7 ± 0·9
Ex. 1	21·1 ± 0·5	24·8 ± 0·5	23·3 ± 0·6	21·8 ± 0·5	21·8 ± 0·5
Ex. 2–8	9·0 ± 0·3	9·2 ± 0·3	9·1 ± 0·3	8·8 ± 0·4	8·8 ± 0·3
LSS	51·4 ± 0·9	62·1 ± 1·1	56·6 ± 1·2	51·7 ± 0·9	55·0 ± 1·2
f seta	36·9 ± 1·0	43·7 ± 1·4	39·2 ± 1·2	39·2 ± 0·8	40·8 ± 1·2
g seta	40·2 ± 1·2	47·9 ± 1·9	43·2 ± 1·2	42·5 ± 0·8	44·4 ± 1·2
h–j seta	13·6 ± 1·1	13·2 ± 1·2	14·5 ± 1·1	15·3 ± 1·4	13·8 ± 1·0

All measurements are expressed as percentages of the carapace length. The measurements are mean values, followed by standard deviations. N = number of observations.

Table 12   Female morphometric characters.

	C. acuta sp. n.	C. australis sp. n.	C. inflata sp. n.	C. rotundata	C. subinflata sp. n.
N	42	4–7	30	20	31
H	46·9 ± 1·0	53·4 ± 1·9	49·9 ± 1·1	48·5 ± 1·0	48·7 ± 1·0
B	41·9 ± 1·8	45·9	49·5 ± 2·1	40·1 ± 2·4	38·0 ± 1·6
F.O.: shaft	26·8 ± 0·9	23·3	26·3 ± 0·7	25·0 ± 0·5	25·7 ± 0·6
capitulum	12·0 ± 0·6	10·8 ± 0·6	12·0 ± 0·5	11·8 ± 0·4	12·5 ± 0·5
total	36·8 ± 1·0	34·0	38·3 ± 0·6	36·8 ± 0·6	36·7 ± 0·7
A1: segs 1 + 2	15·0 ± 0·4	11·9	15·0 ± 0·7	13·3 ± 0·4	12·8 ± 0·5
a–d setae	16·6 ± 1·2	14·9 ± 0·9	17·7 ± 1·2	17·7 ± 1·8	17·4 ± 1·4
e seta	31·1 ± 0·8	36·7 ± 0·8	35·4 ± 0·8	32·8 ± 1·1	35·3 ± 0·7
A2: protop.	46·4 ± 0·7	47·2 ± 0·8	46·5 ± 0·6	43·4 ± 0·8	45·4 ± 0·8
Ex. 1	20·2 ± 0·4	23·1 ± 0·4	22·7 ± 0·4	20·3 ± 0·9	20·8 ± 0·5
Ex. 2–8	8·4 ± 0·3	8·5 ± 0·5	8·9 ± 0·3	8·4 ± 0·3	8·4 ± 0·2
LSS	38·7 ± 0·9	48·7 ± 0·8	43·6 ± 0·6	40·8 ± 0·8	43·2 ± 1·1
f–j setae	18·6 ± 0·9	23·6 ± 1·9	23·1 ± 1·2	22·5 ± 1·6	22·5 ± 1·1

All measurements are expressed as percentages of the carapace length. The measurements are means, followed by standard deviations. N = number of observations.

Table 13 Morphological details of five *skogsbergi* complex species.

	C. acuta sp. n.	C. australis sp. n.	C. inflata sp. n.	C. rotundata	C. subinflata sp. n.
♂A1:					
b seta spines: ant. side	7–10 : 4–7	9–12 : 3–8	6–11 : 5–12	6–8 : 4–7	6–11 : 4–11
post. side	6–13	12–18	3–11	1–2	7–8
d seta spines	9–15 : 3–7	11–17 : 3–4	8–13 : 2–5	9–12 : 3–4	8–17 : 3–5
e seta spines	20–24	20–23	19–26	14–18	18–22
♂A2:					
f seta spines	1–2	3–5	2–3	2–5	3–5
g seta spines	0–5	1–4	4–7	0–3	2–3
Penis muscles	2–4	5	2–6	4–5	5
♀A1:					
e seta spines: ant. side	20–23	36–40	34–44	20–33	31–45
post. side	25–35	35–42	28–38	25–35	25–35
Mandibular teeth:					
cutting edge	12–14	14–16	11–15	12–14	13–15
distal list	18–20	20–21	17–22	18–20	17–25
proximal list	15–20	15–18	20–25	15–20	20–21

The first range of numbers given for ♂A1 b and d setae refers to the more proximal, closely spaced spines, the second range is for the more distal, widely spaced spines. Note that the ♂A1 f and g seta spines and some of the spines on the ♀A1 e seta and the ♂A1 b and d setae can be seen only be carefully examining these setae under high magnification.
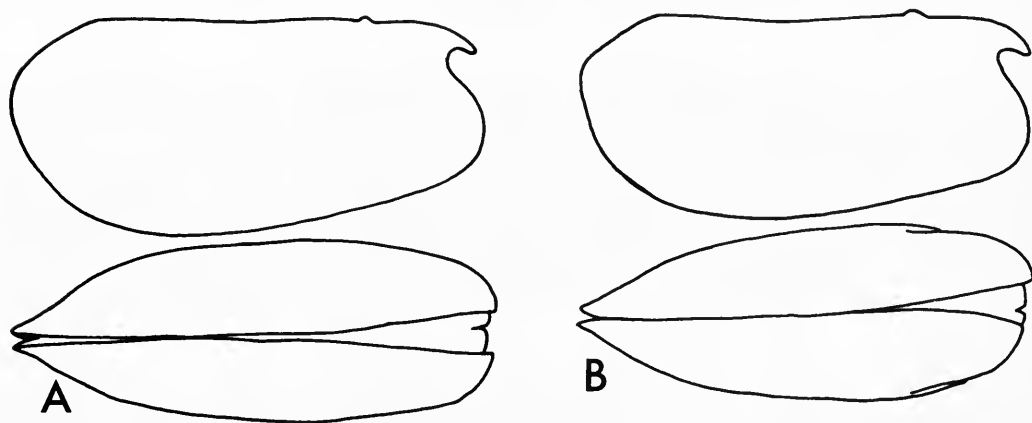
Fig. 2 Lateral and ventral carapace outlines, *Conchoecia glandulosa*, Station 9756 haul 7: A, ♀; B, ♂. Scale 1·0 mm.
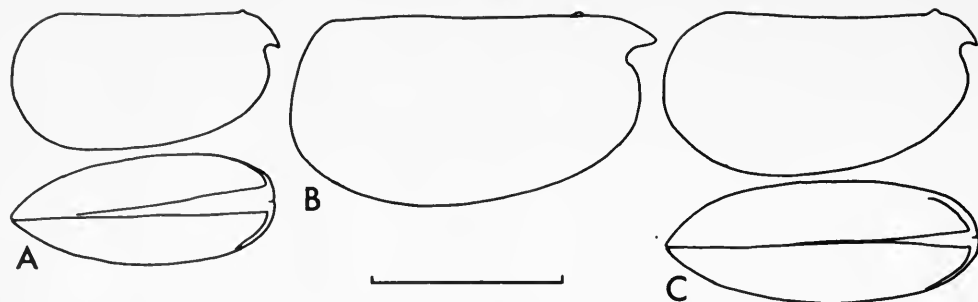
Fig. 3 Lateral and ventral carapace outlines: A, *Conchoecia skogsbergi* ♂, Station 2501; B, *C. abyssalis* ♂ (after Rudyakov, 1962); C, *C. skogsbergi* ♀, 2501. Scale 1·0 mm.
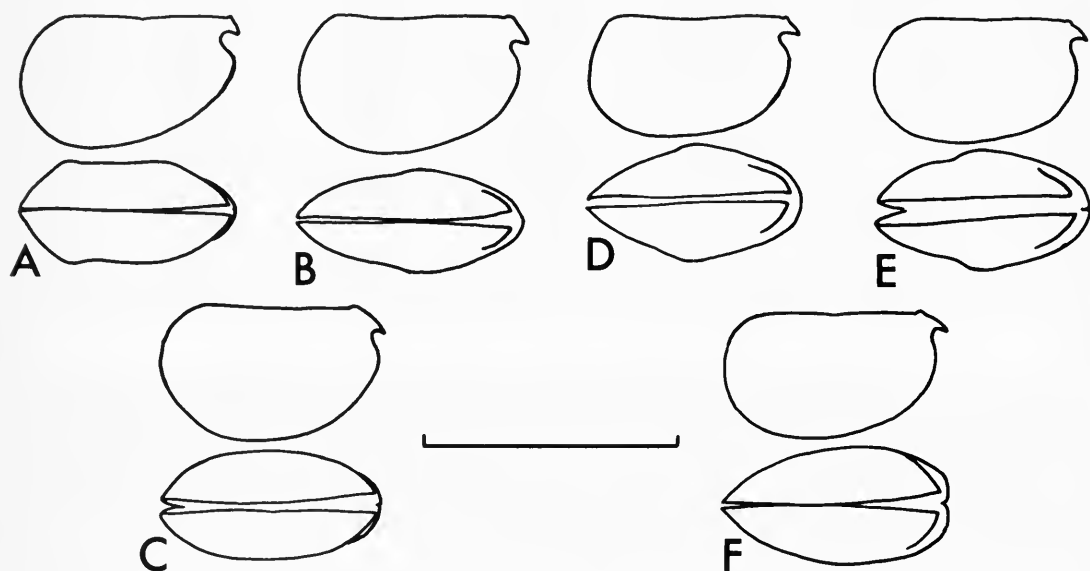
Fig. 4 Lateral and ventral carapace outlines: A, *Conchoecia nasotuberculata* ♀, Station 6665 haul 6; B, *C. kyrtophora* ♀, 6665 haul 33; C, *C. teretivalvata* ♀, 7709 haul 2; D, *C. naso-tuberculata* ♂, 6665 haul 6; E, *C. kyrtophora* ♂, 6665 haul 6; F, *C. teretivalvata* ♂, 7709 haul 2. Scale 1·0 mm.
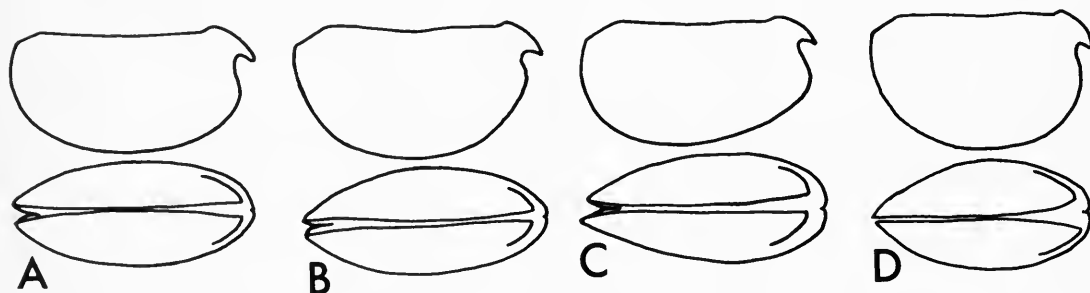
Fig. 5 Lateral and ventral carapace outlines: A, *Conchoecia pusilla* ♀, Station 7486; B, *C. isochiera* ♀, 1781; C, *C. pusilla* ♂, 7481; D, *C. isochiera* ♂, 1781. Scale 1·0 mm.
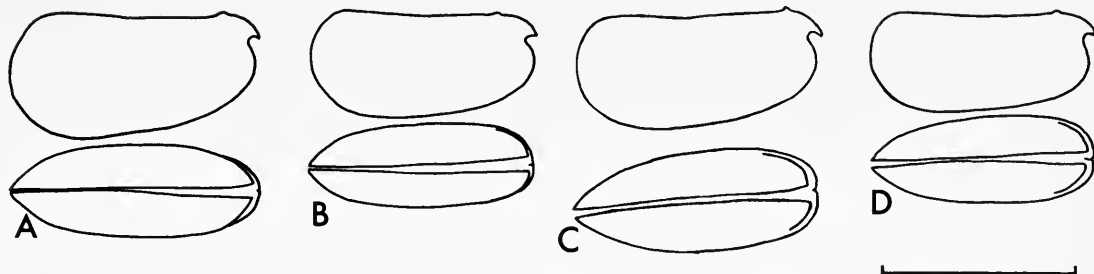
Fig. 6   Lateral and ventral carapace outlines: A, *Conchoecia fowleri* sp. nov. ♀, Station 7711 haul 32; B, *C. discoveryi* sp. nov. ♀, 7709 haul 63; C, *C. fowleri* sp. nov. ♂, 7711 haul 32; D, *C. discoveryi* sp. nov. ♂, 7709 haul 35. Scale 1·0 mm.
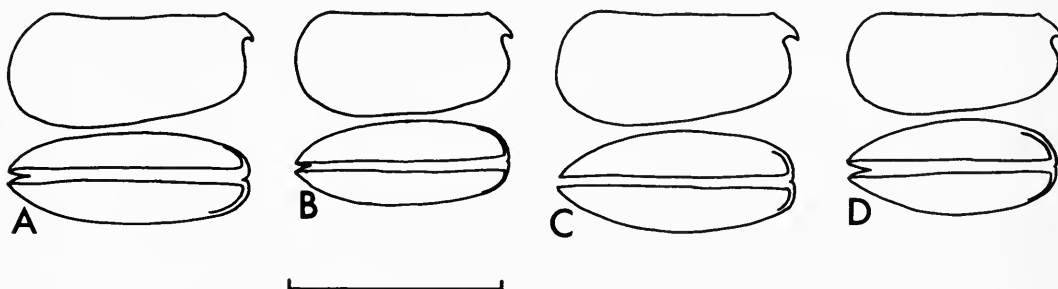
Fig. 7   Lateral and ventral carapace outlines: A, *Conchoecia wolferi* sp. nov. ♀, Station 6665 haul 4; B, *C. obtusa* sp. nov. ♀, 7856 haul 2; C, *C. wolferi* sp. nov. ♂, 6665 haul 4; D, *C. obtusa* sp. nov. ♂, 6665 haul 4. Scale 1·0 mm.
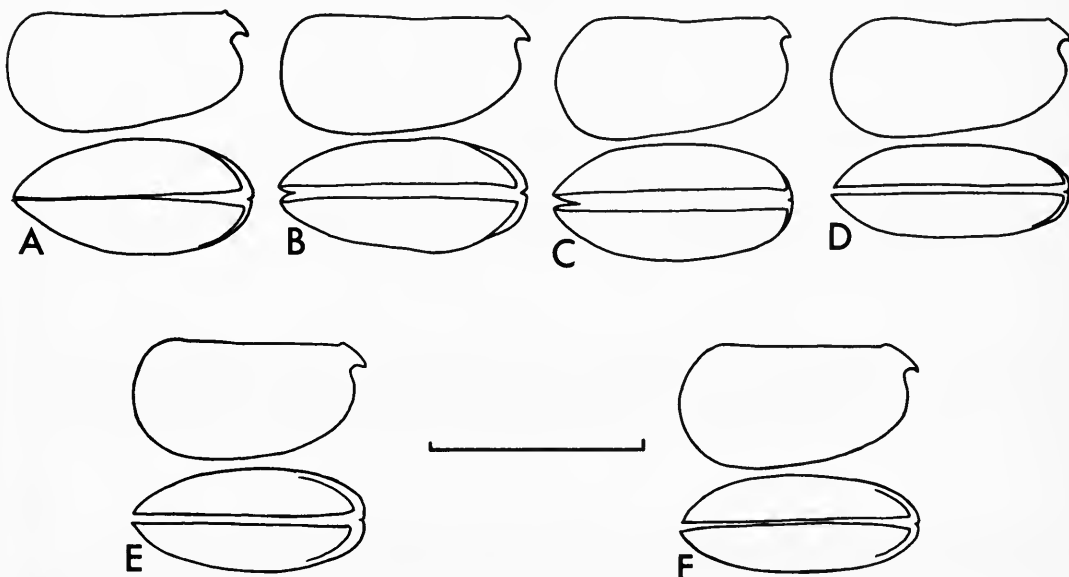
Fig. 8   Lateral and ventral carapace outlines: A, *Conchoecia inflata* sp. nov. ♂, Station 7856 haul 21; B, *C. subinflata* sp. nov. ♂, 7711 haul 23; C, *C. inflata* ♀, 7856 haul 21; D, *C. subinflata* sp. nov. ♀, 7711 haul 23; E, *C. australis* sp. nov. ♂, *Gauss* Station 18.12.01; F, *C. australis* sp. nov. ♀, *Gauss* Station 18.12.01. Scale 1·0 mm.
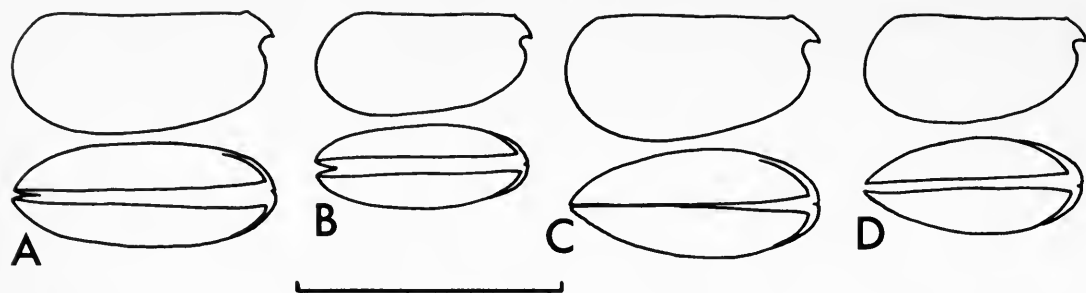
Fig. 9 Lateral and ventral carapace outlines: A, *Conchoecia acuta* sp. nov. ♀, Station 7089 haul 19; B, *C. rotundata* ♀, 7856 haul 18; C, *C. acuta* sp. nov. ♂, 7089 haul 19; D, *C. rotundata,* 7856 haul 72. Scale 1·0 mm.
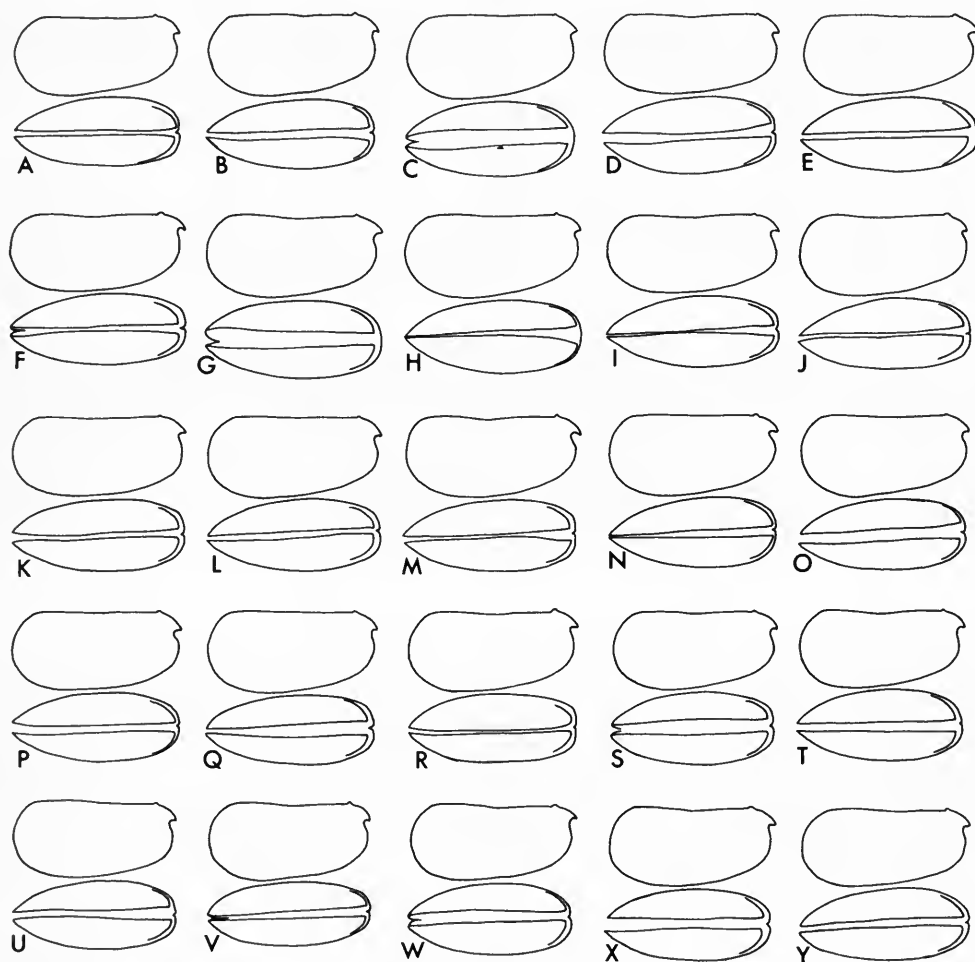
Fig. 10 *Conchoecia fowleri* sp. nov. ♂♂, lateral and ventral carapace outlines: A–F, Station 7709 haul 3; G, H, 7709 haul 36; I, K–M, 7711 haul 32; J, 7711 haul 6; N, O, 7406 haul 24; P–R, 7406 haul 44; S, 7856 haul 4; T, 7856 haul 10; U–Y, 7856 haul 13. Scale 1·0 mm.
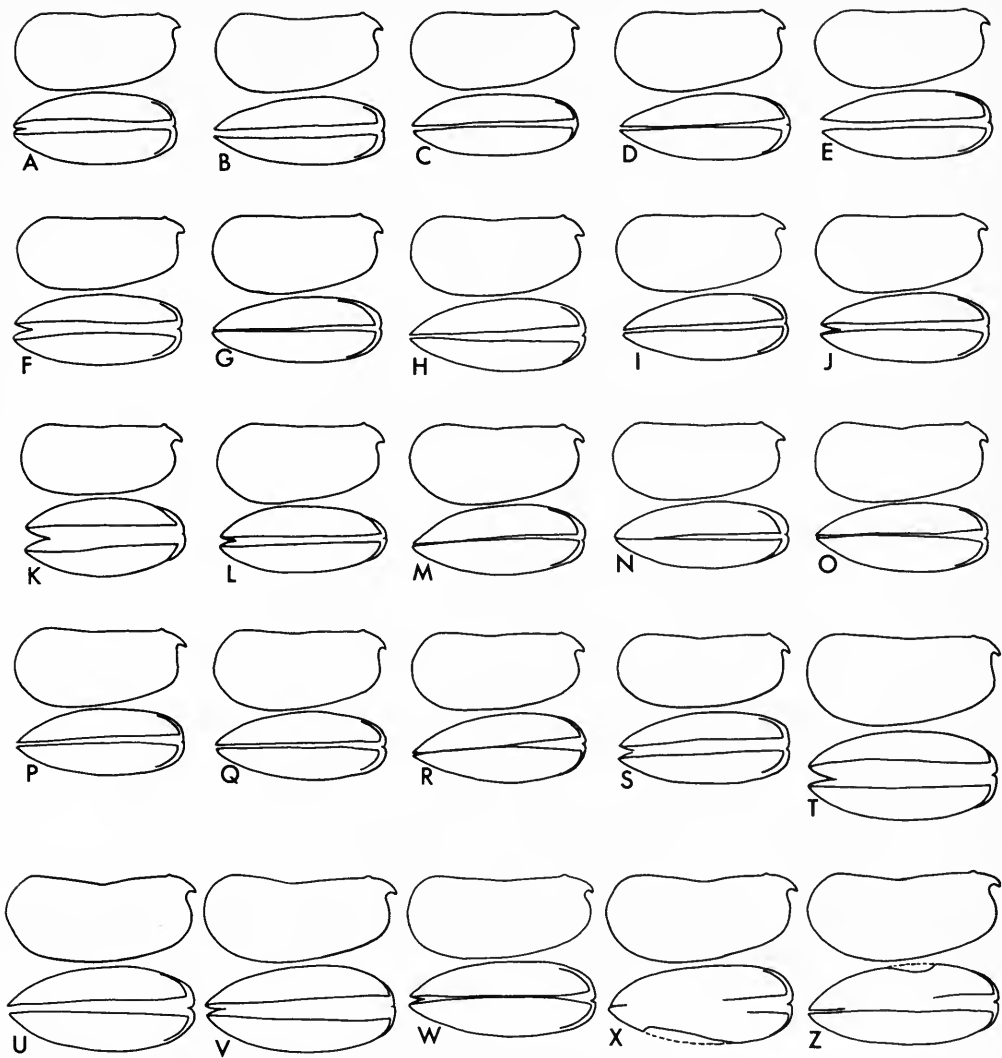
Fig. 11 Lateral and ventral outlines of male carapaces: A–S, *Conchoecia fowleri* sp. nov.; A, B, Station 7089 haul 4; C–J, 7089 haul 14; K, L, R, S, 6665 haul 27; M–Q, 6665 haul 22: T–Z, *Conchoecia fowleri* form A: T, 7803 haul 11; U, X–Z, 6665 haul 26; V, 6665 haul 24; Scale 1·0 mm.
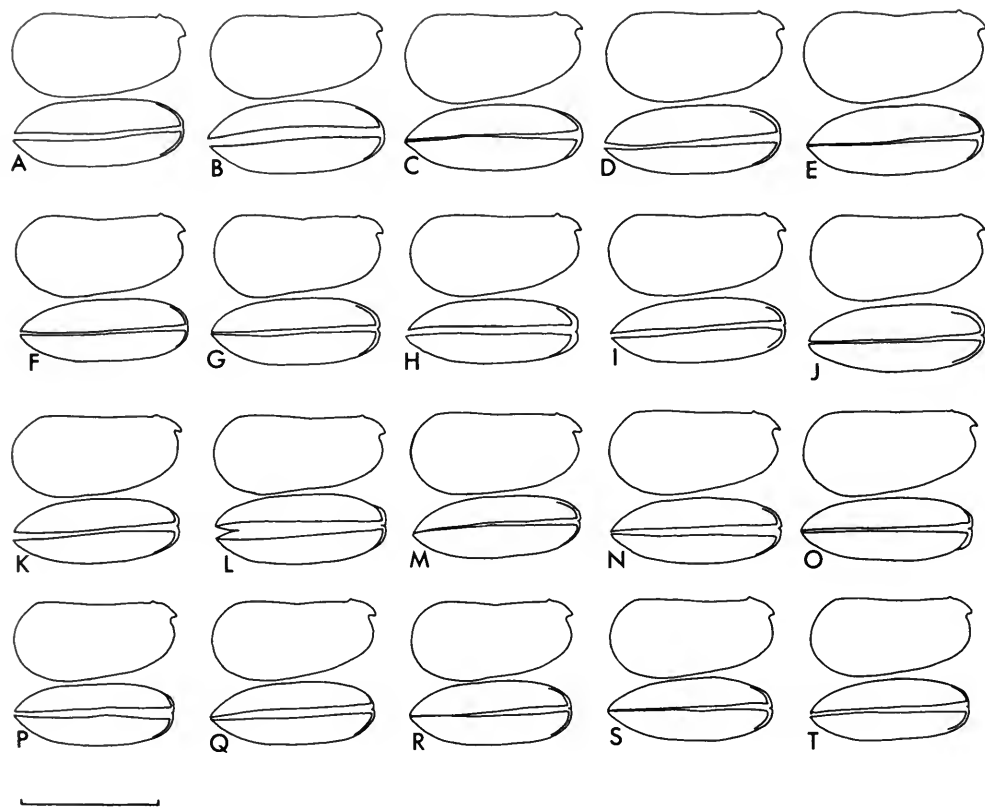
Fig. 12 *Conchoecia fowleri* sp. nov. ♀♀, lateral and ventral carapace outlines: A–E, Station 7709 haul 36; F–J, 7711 haul 32; K, N, O, 7406 haul 24; L, 7406 haul 27; M, 7406 haul 44; P, 7856 haul 4; Q–T, 7856 haul 13. Scale 1·0 mm.
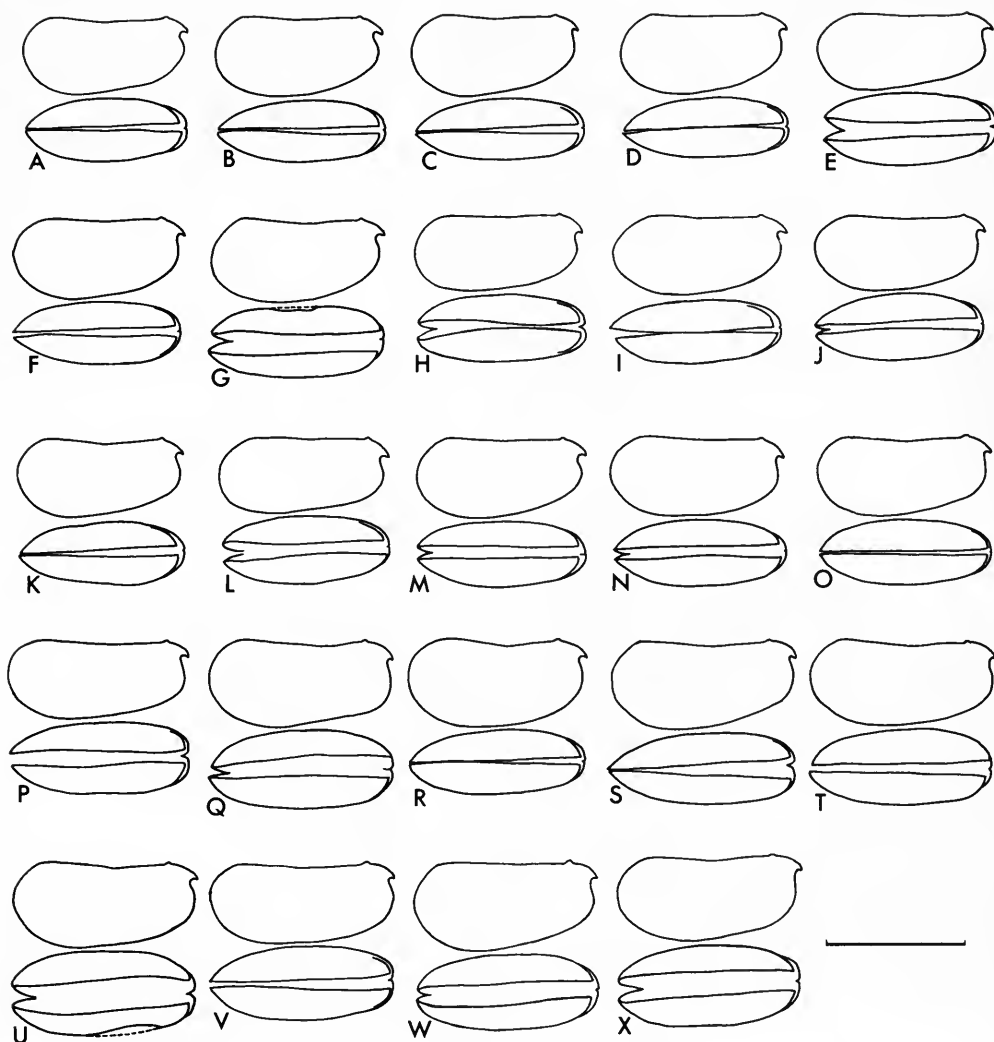
Fig. 13 Lateral and ventral outlines of female carapaces: A–O, *Conchoecia fowleri* sp. nov.; A–D, F, H, I, Station 7089 haul 14; E, G, 7089 haul 34; J, N, O, 6665 haul 23; K–M, 6665 haul 21; P–X, *Conchoecia fowleri* form A; P, 6665 haul 28; Q, 6665 haul 24; R, V, 6665 haul 21; S, 6665 haul 32; T, U, 6665 haul 26; W, X, 7089 haul 7. Scale 1·0 mm.
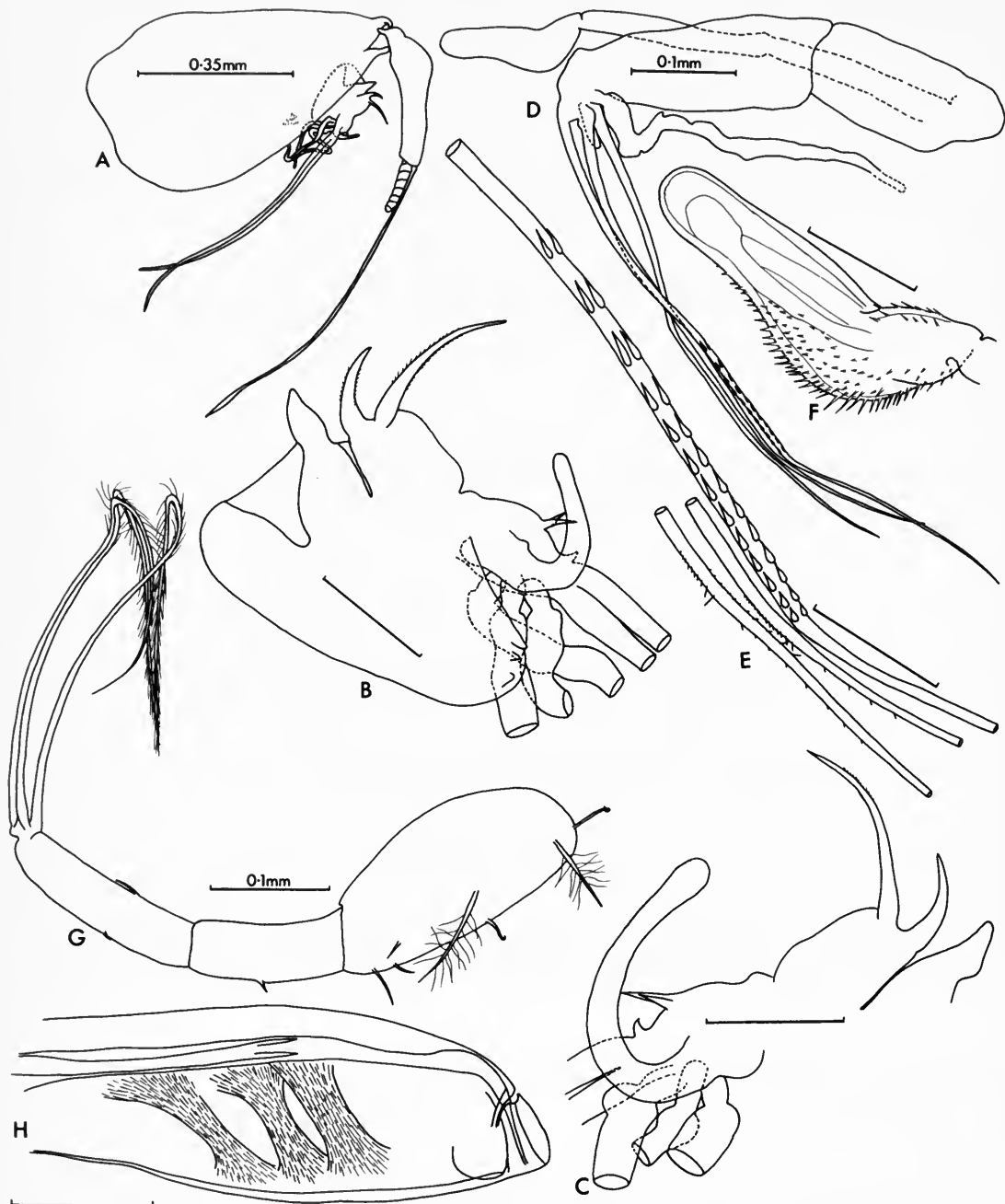
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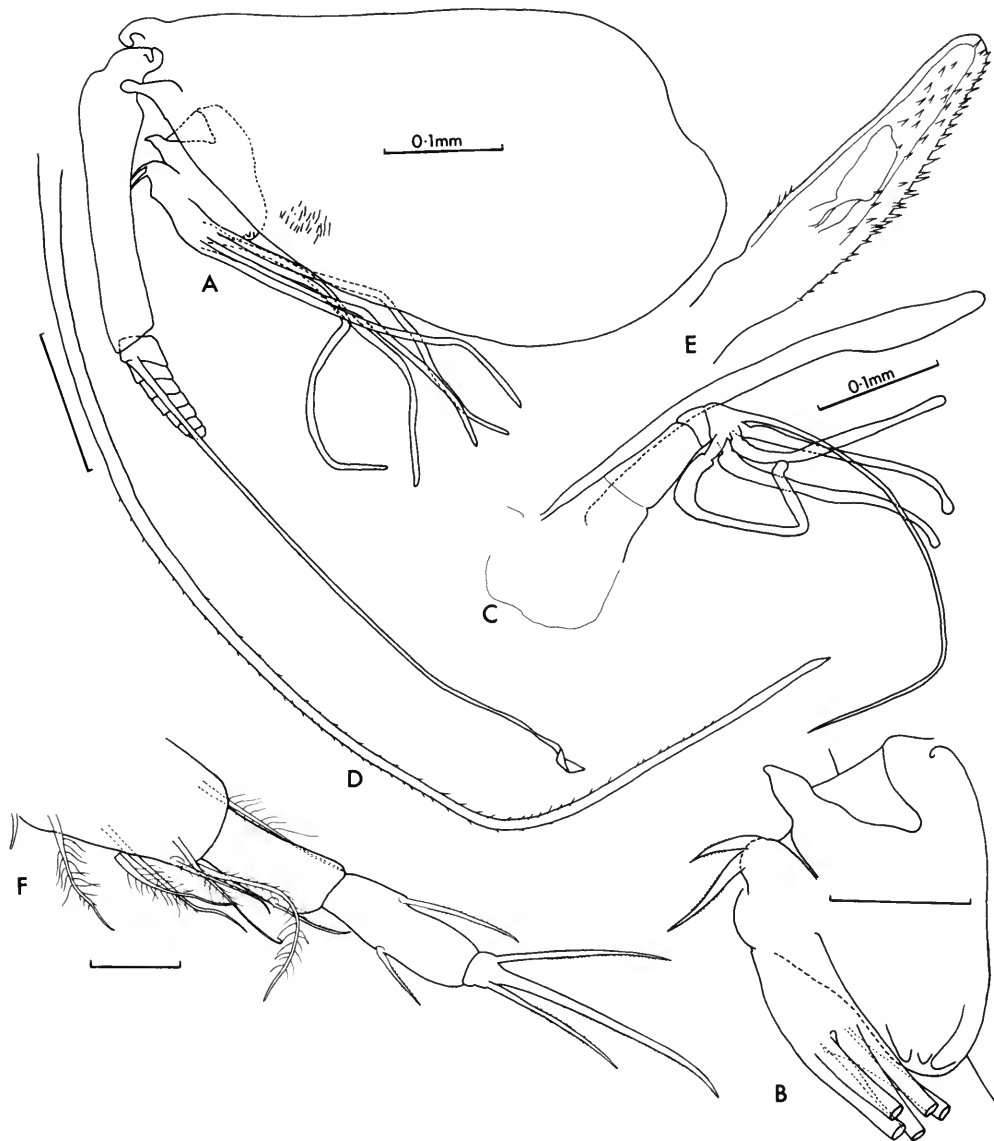
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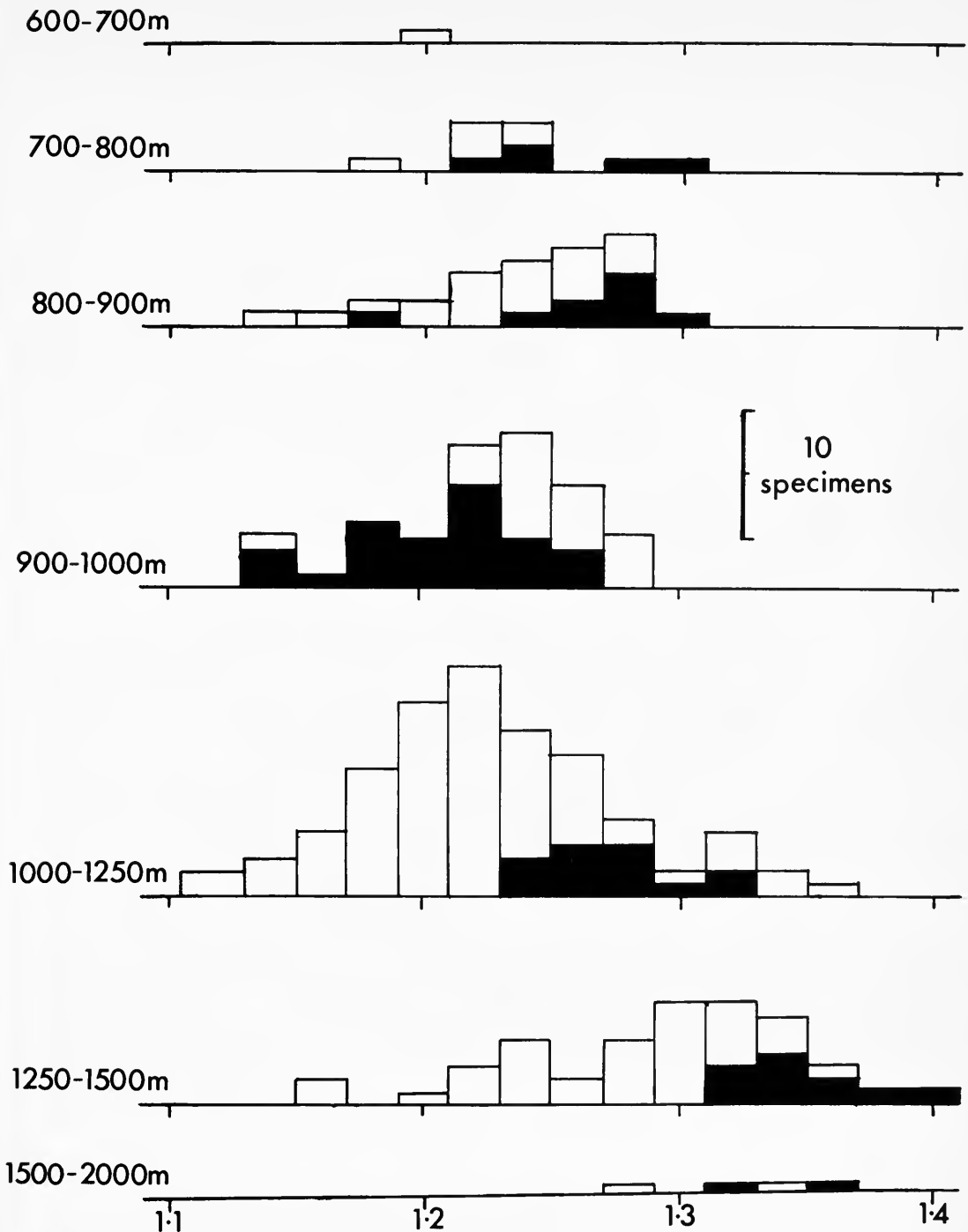
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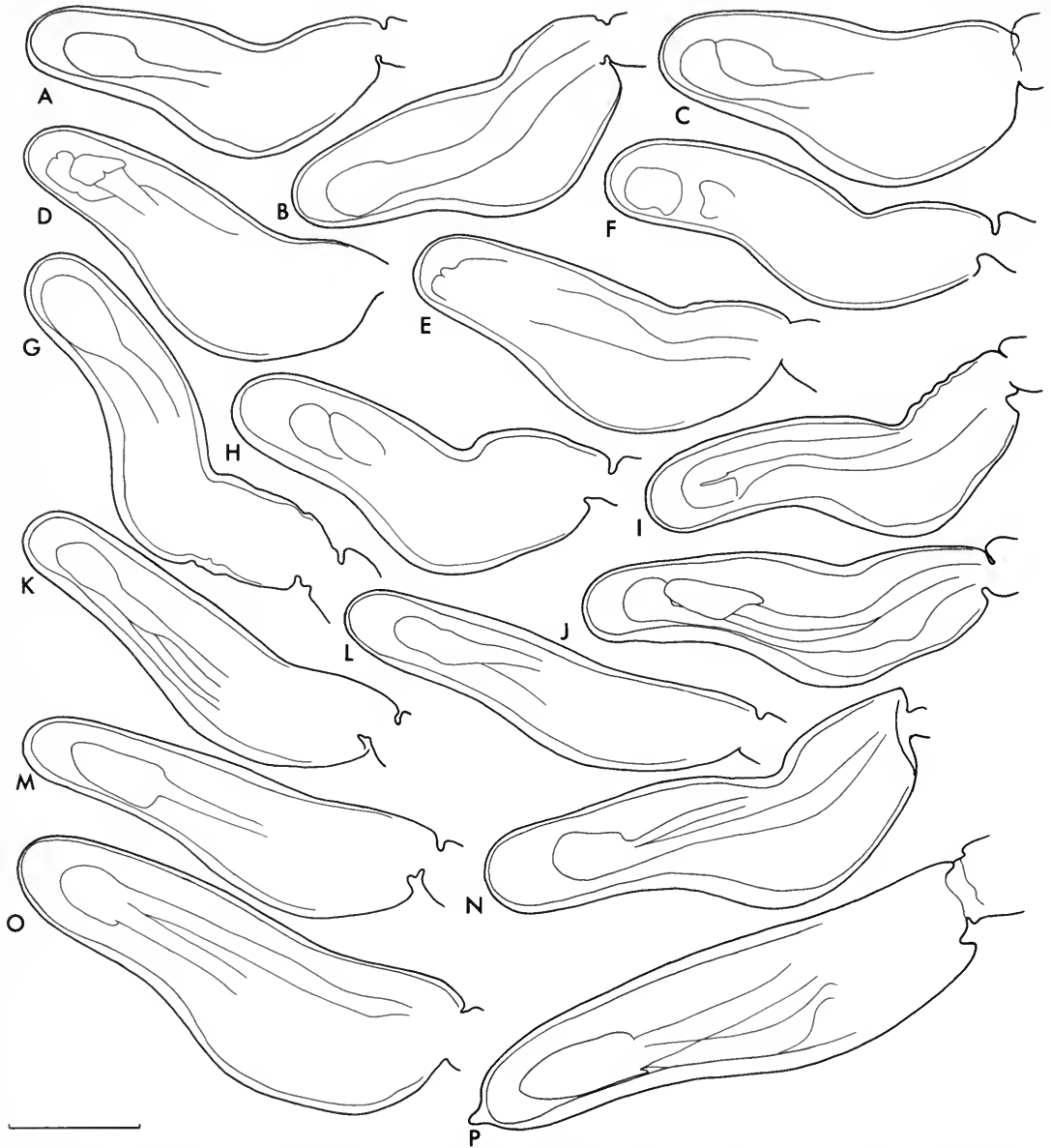
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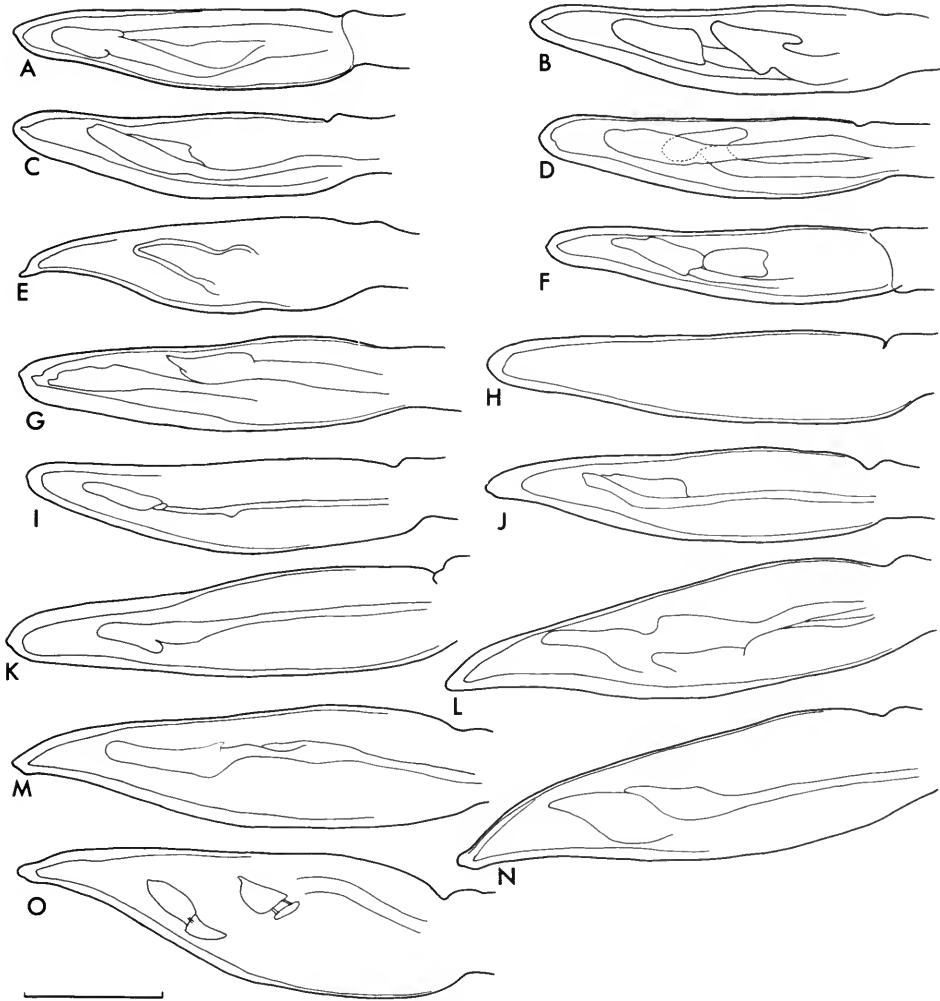
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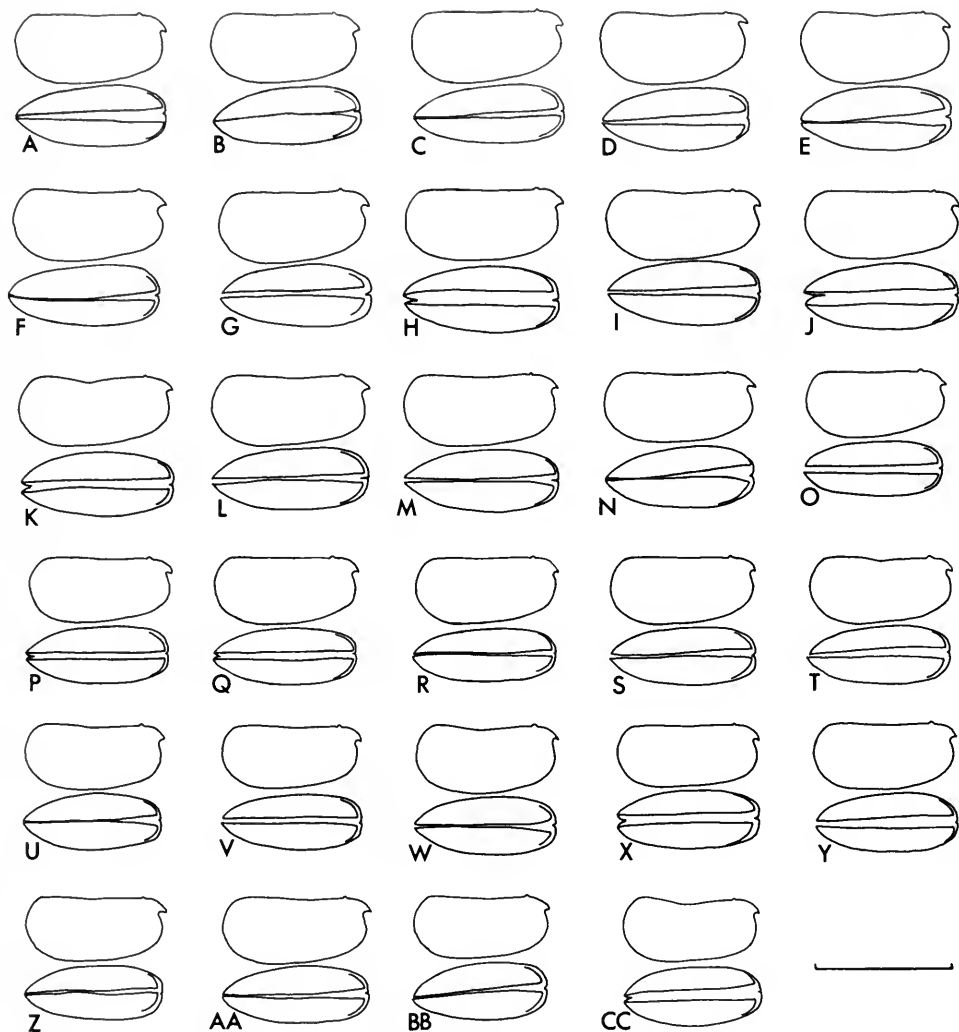
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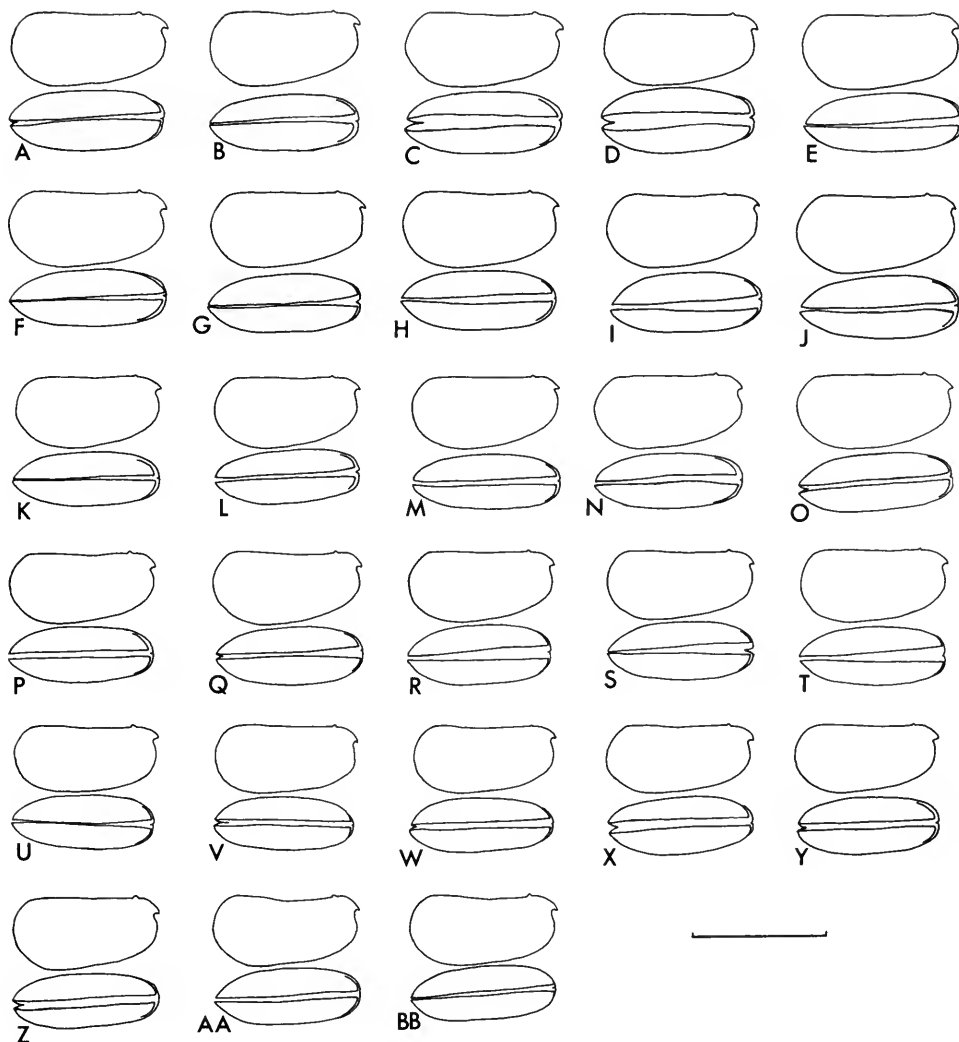
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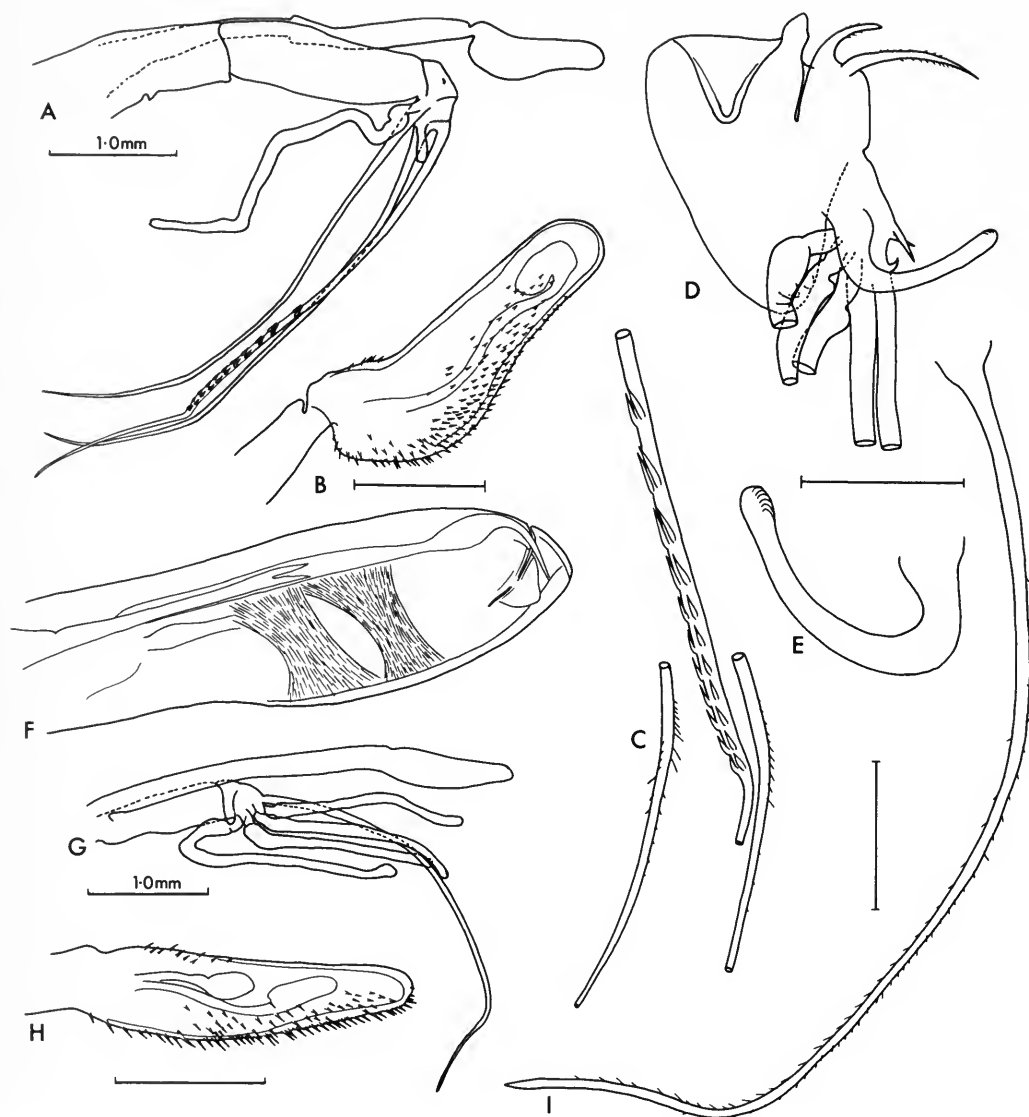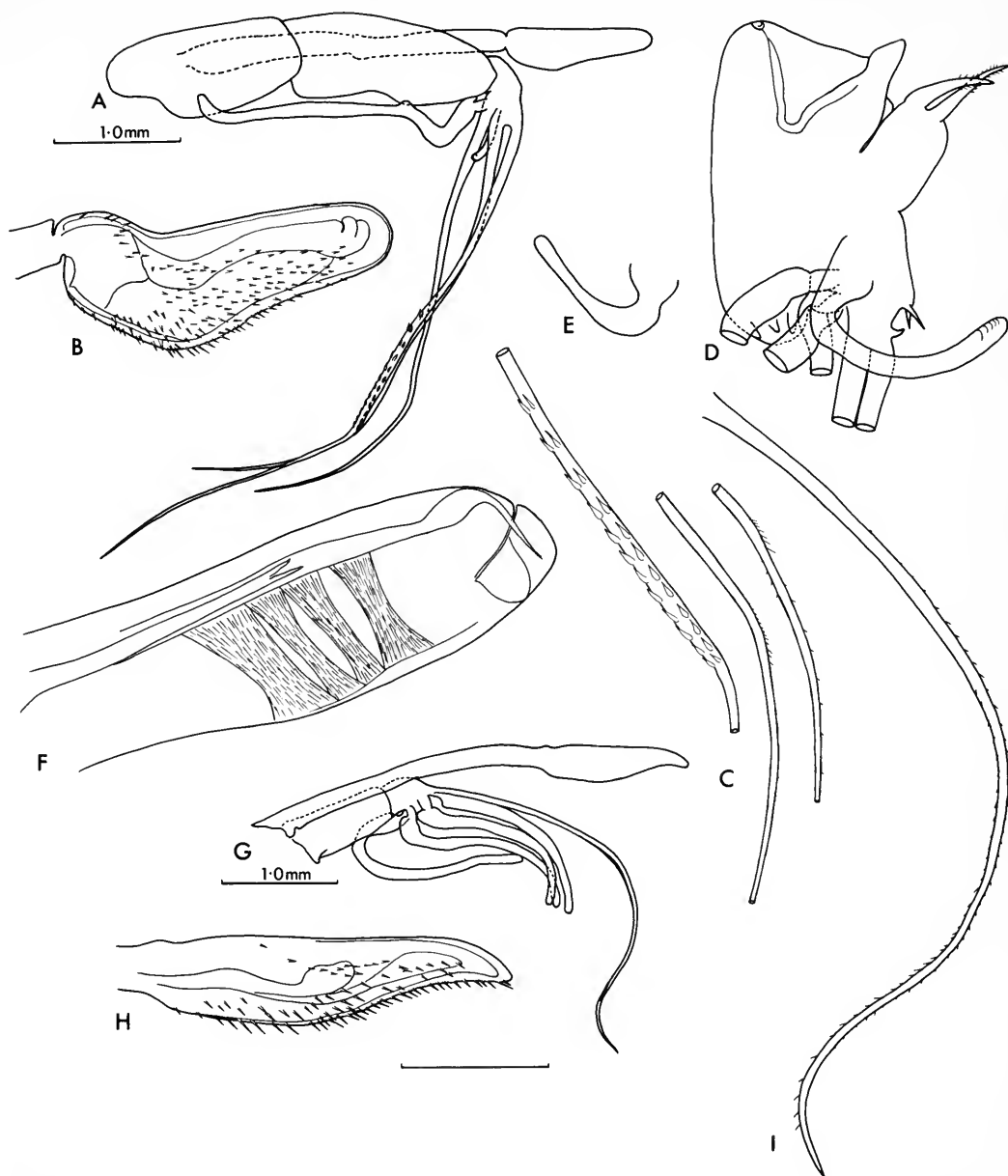
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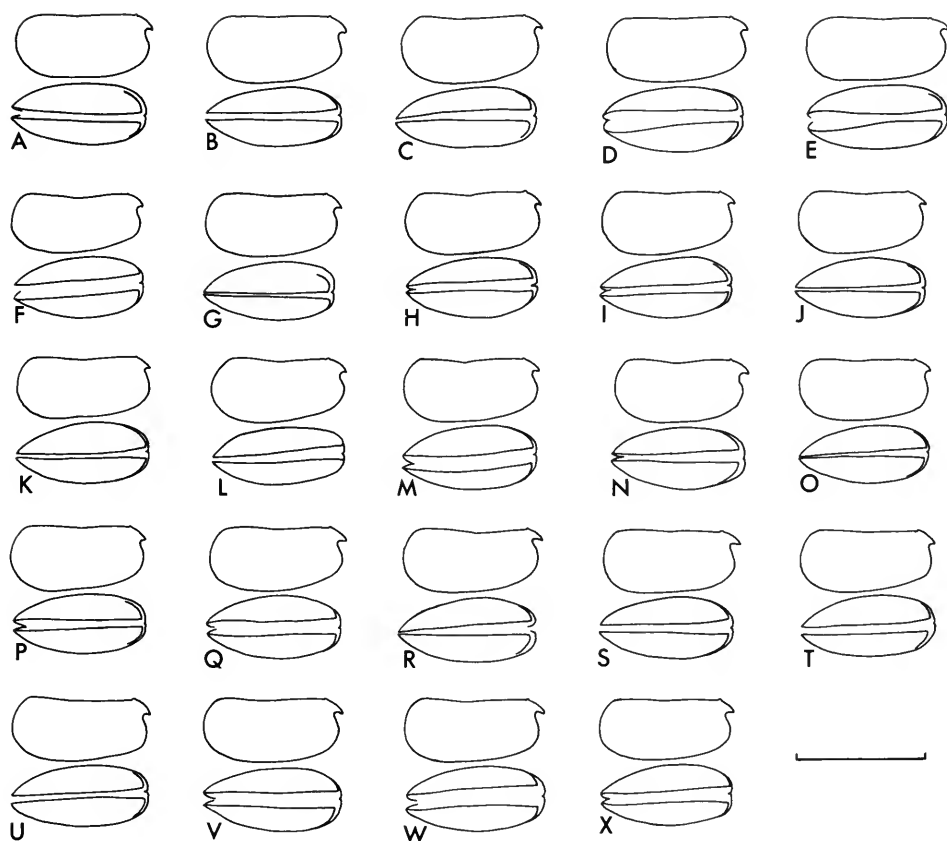
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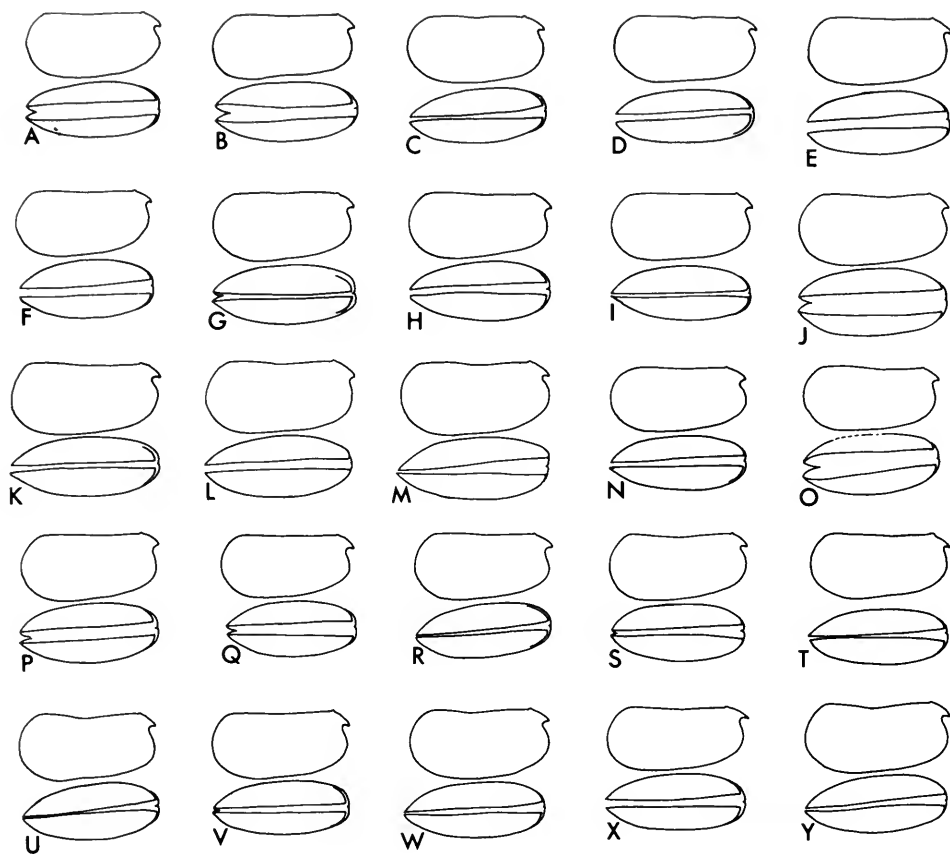
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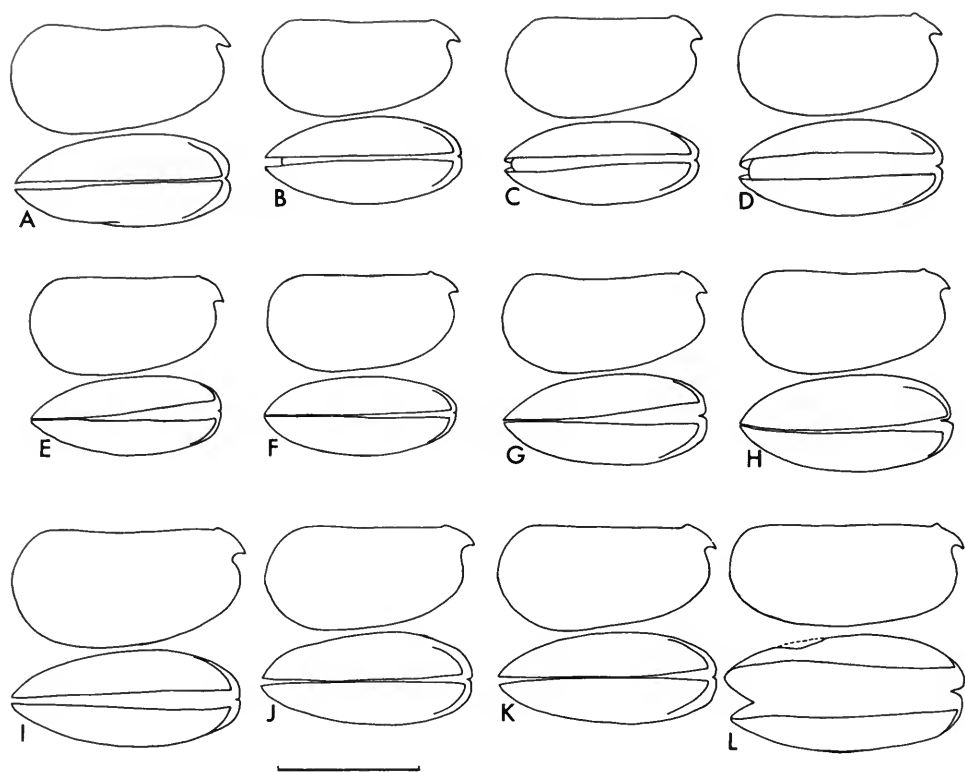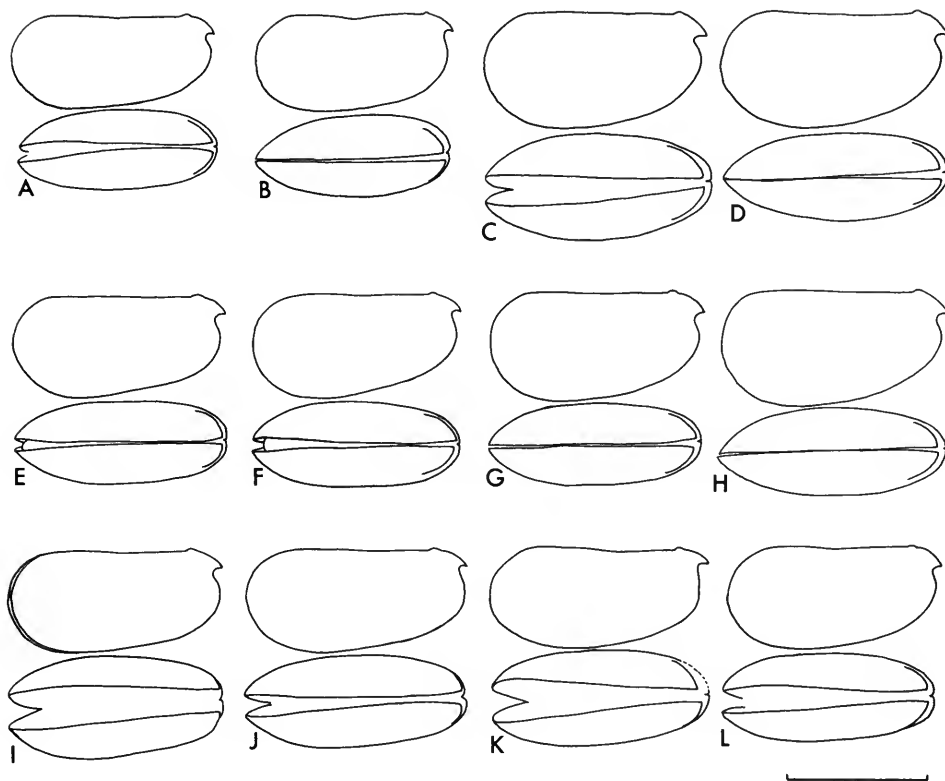
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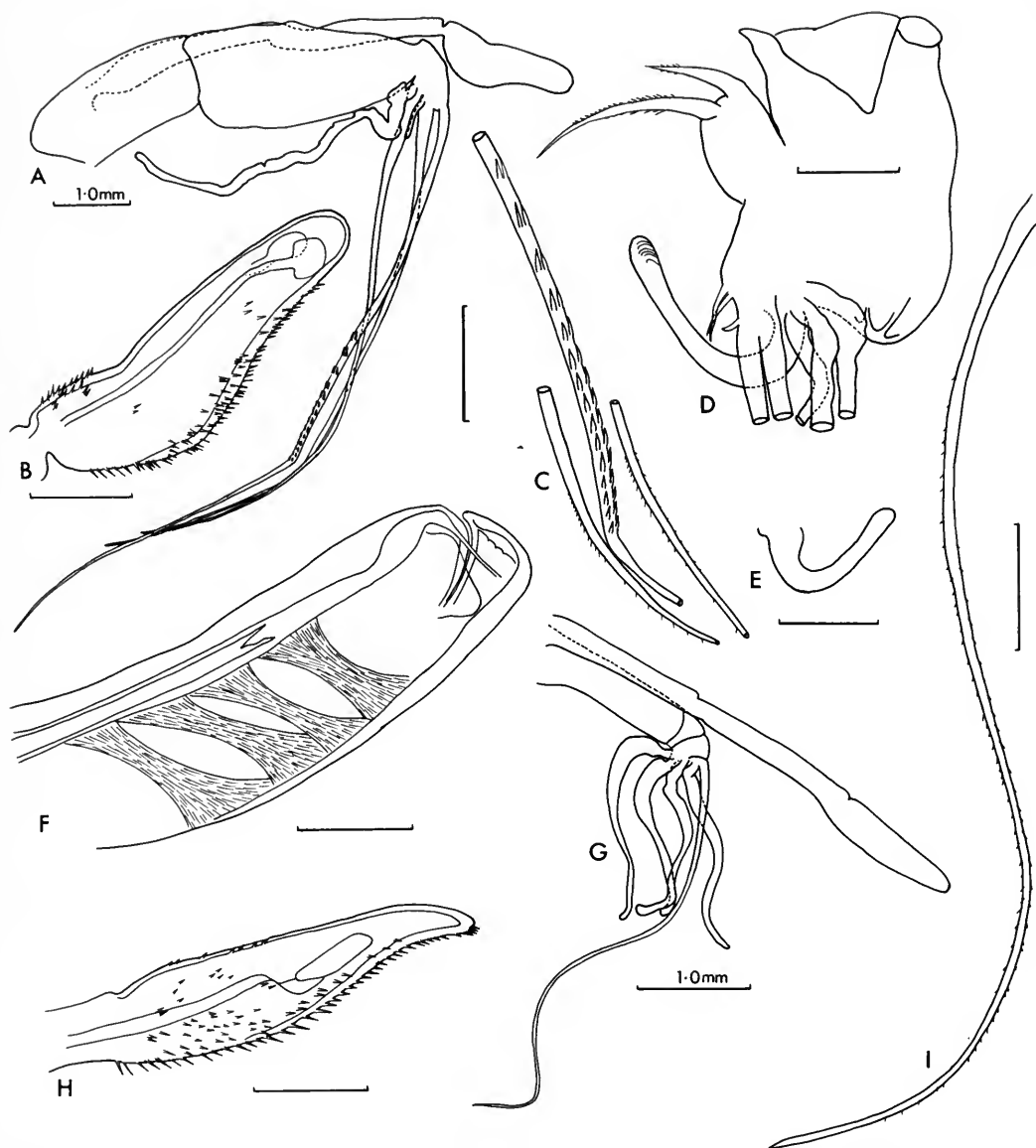
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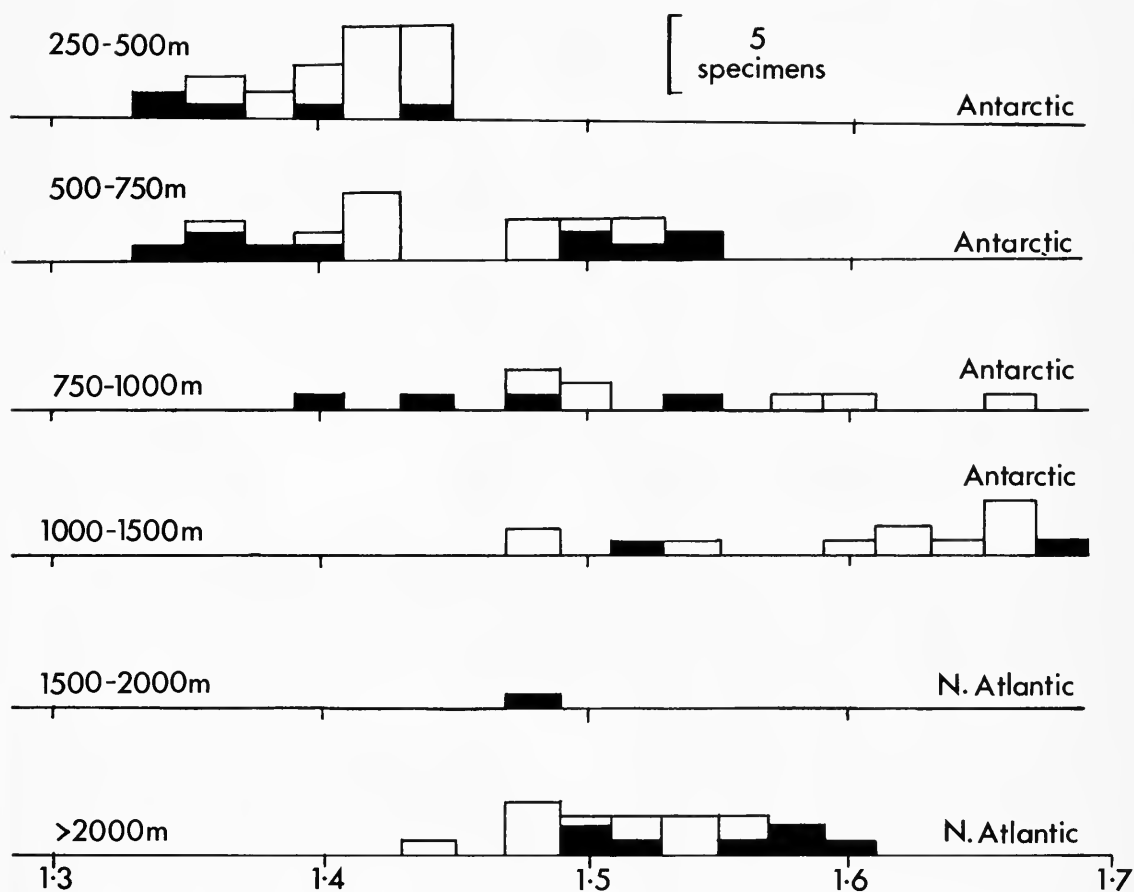
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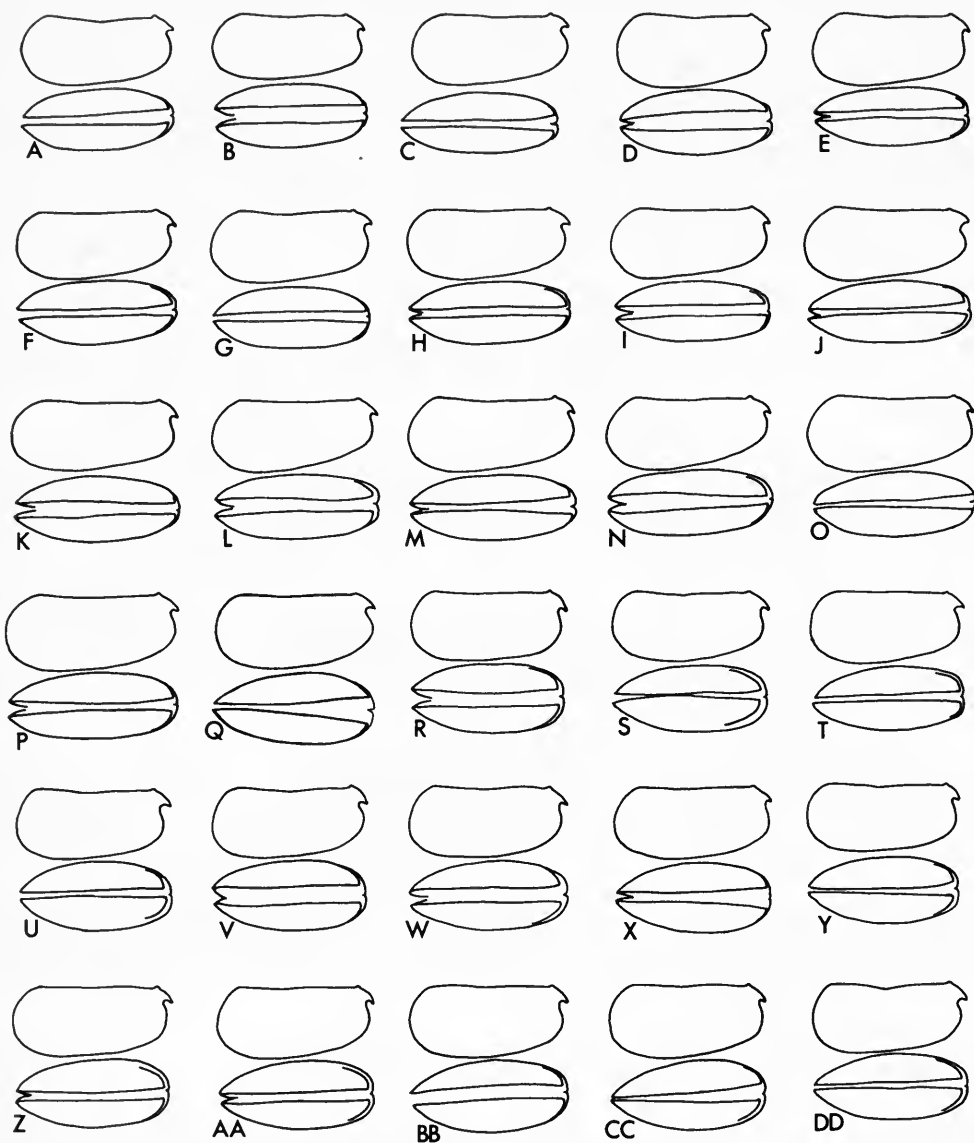
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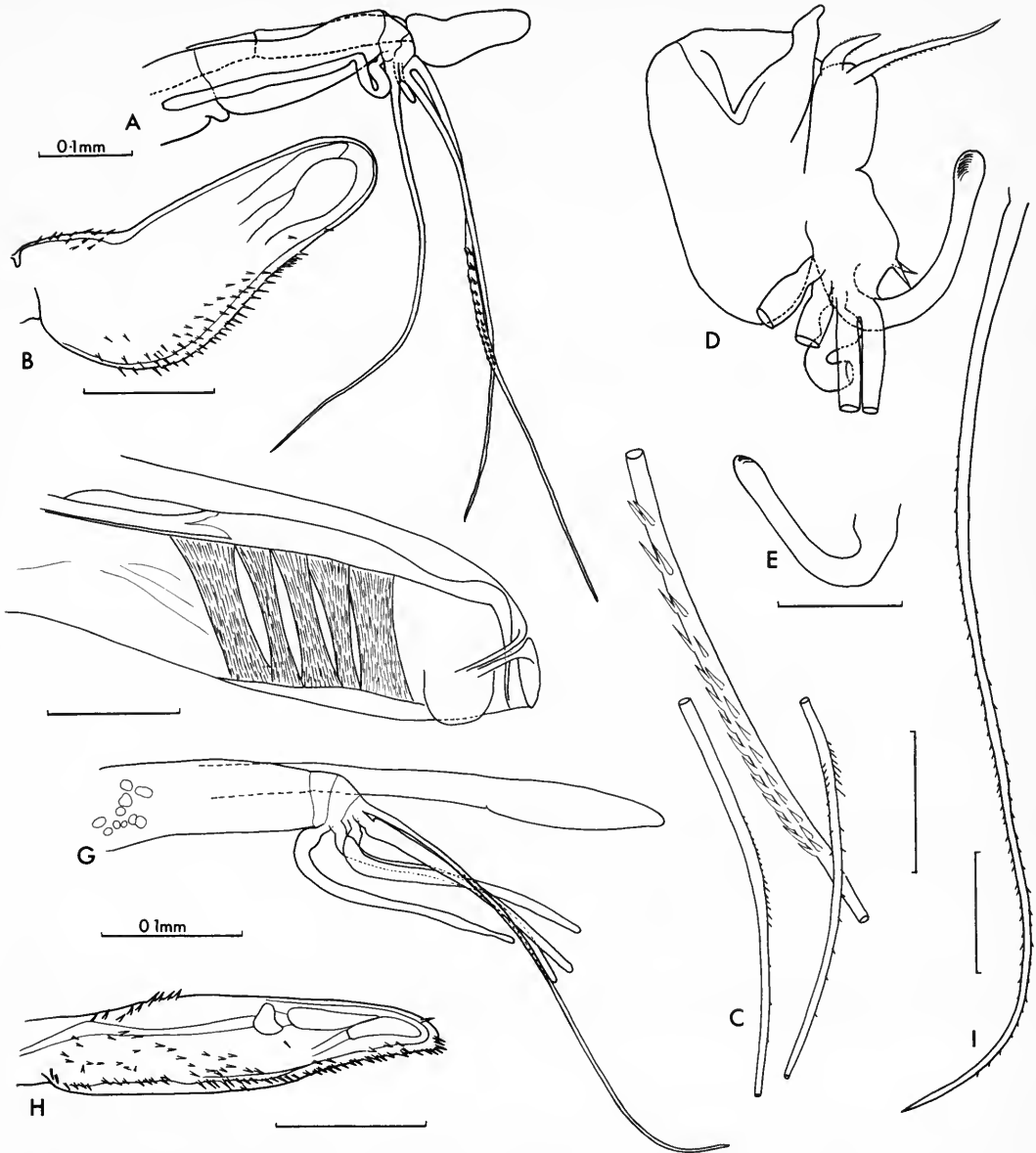
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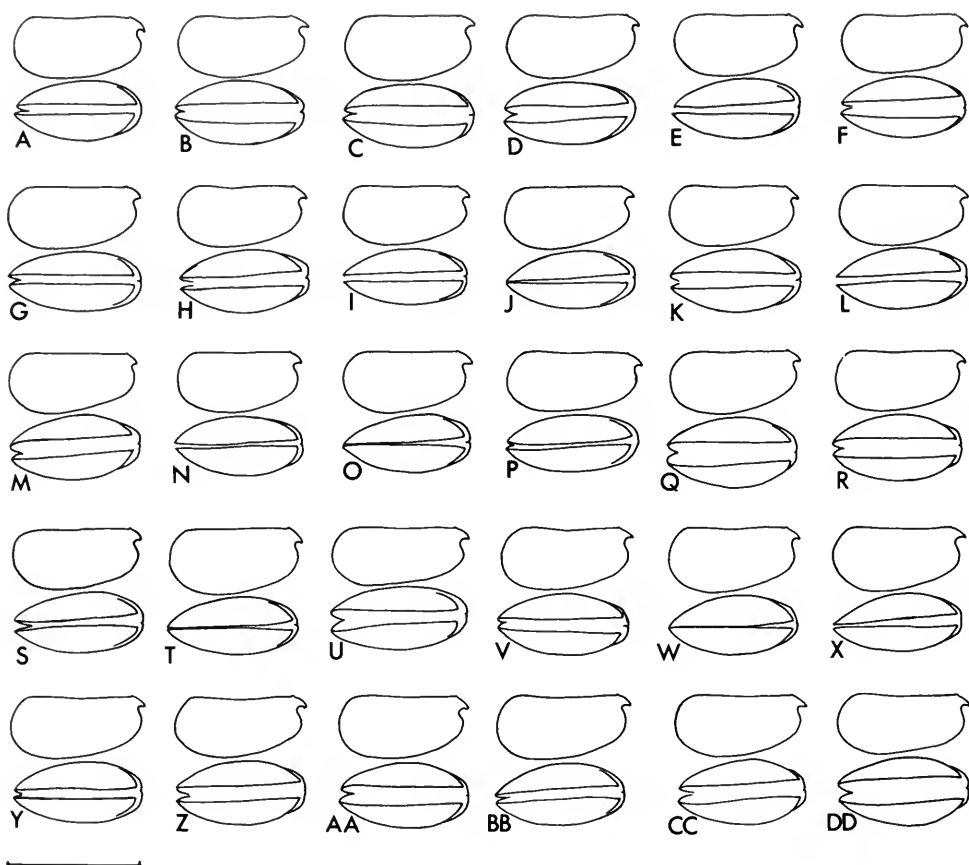
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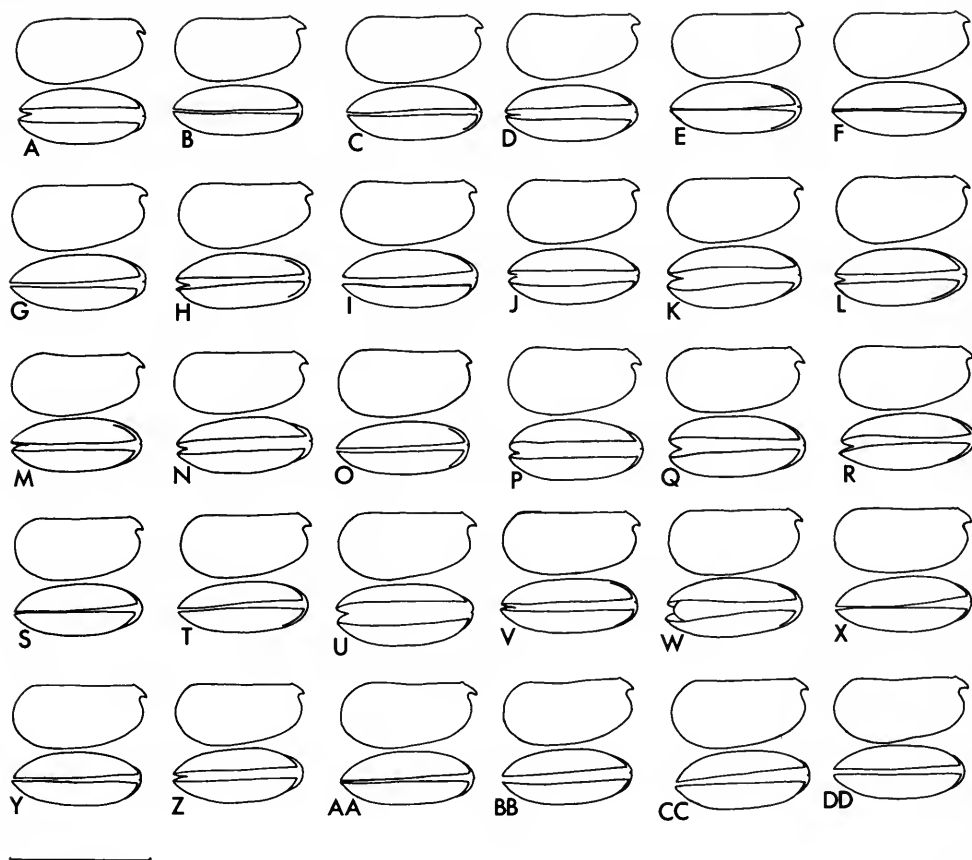
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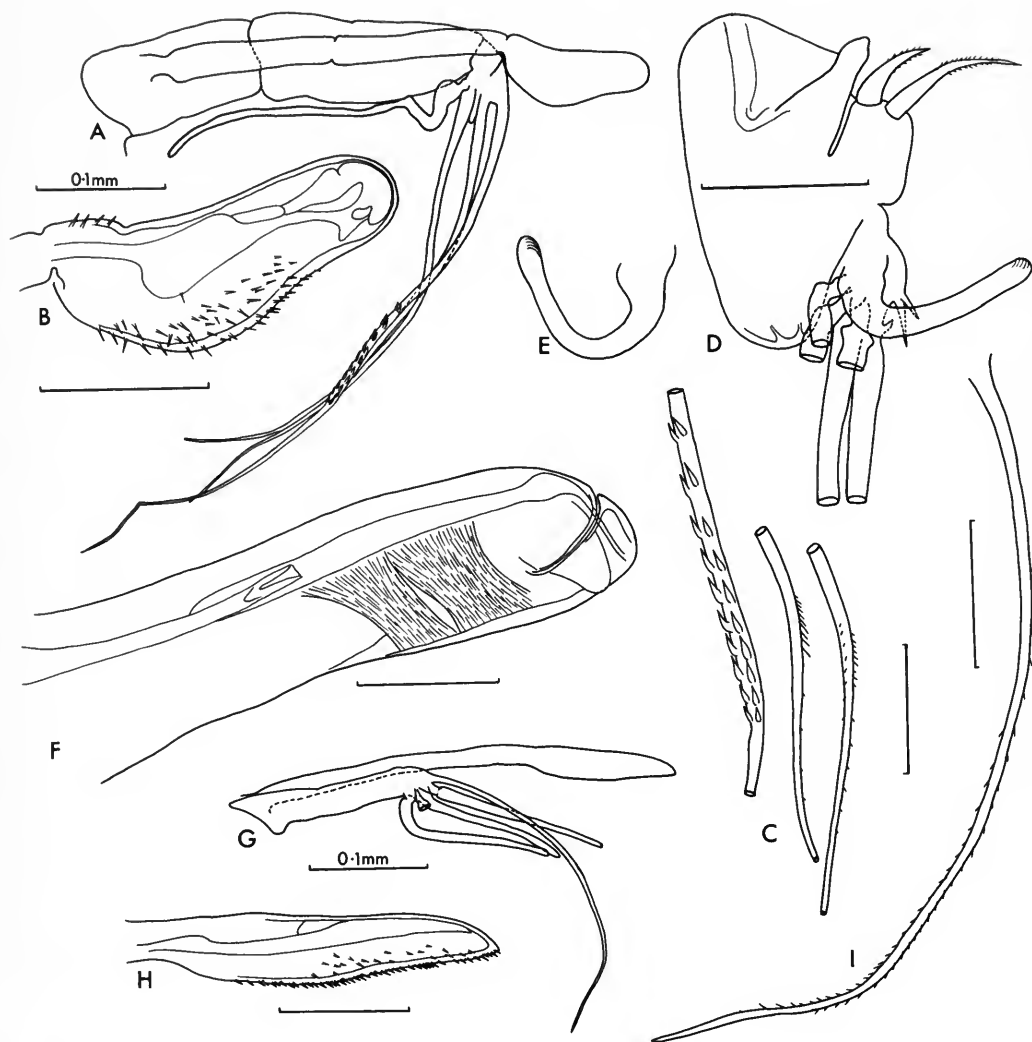
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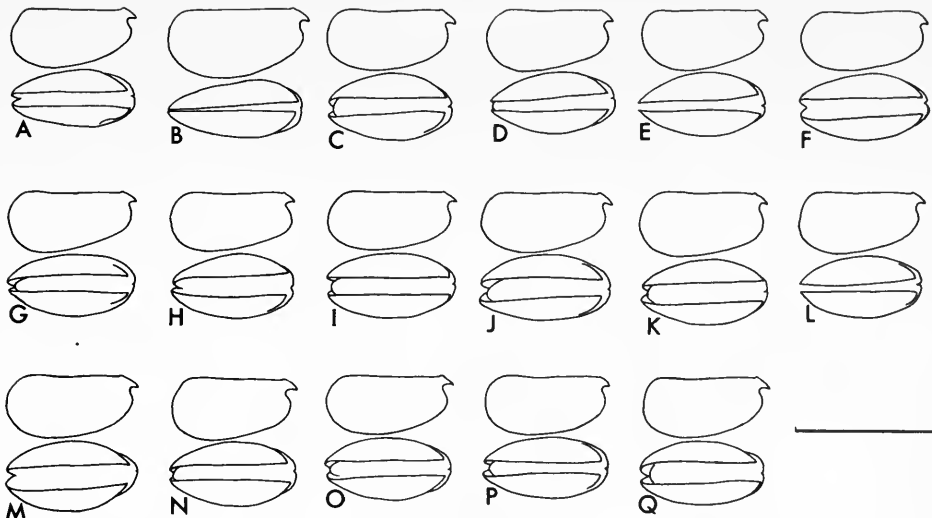
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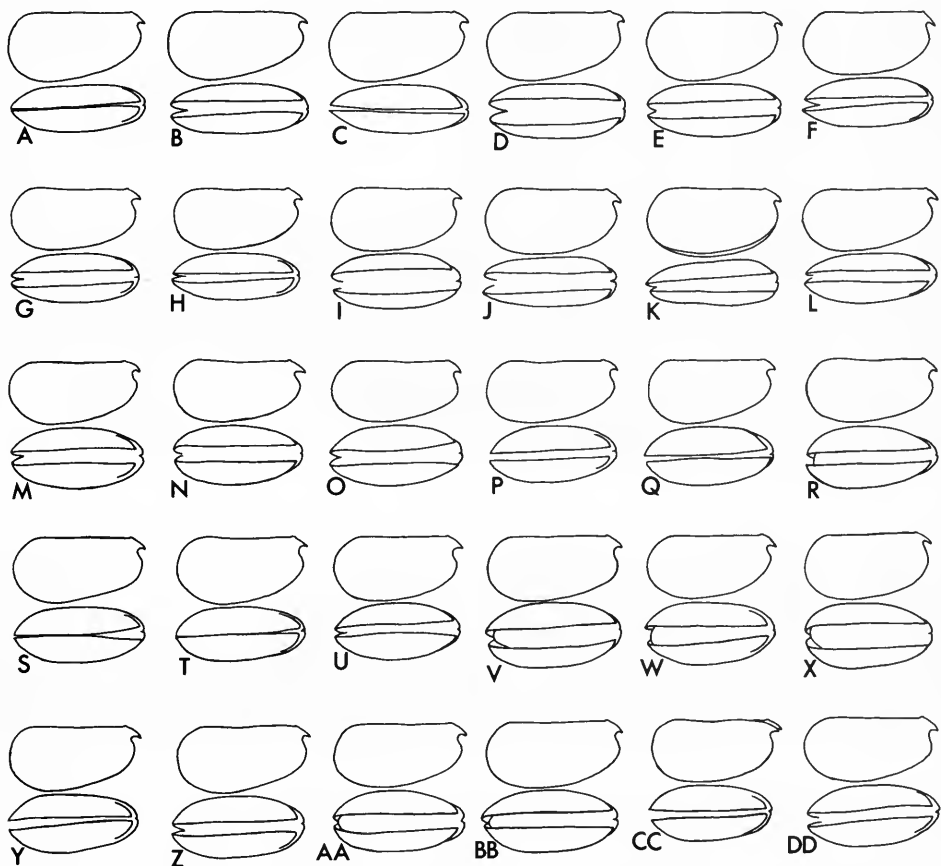

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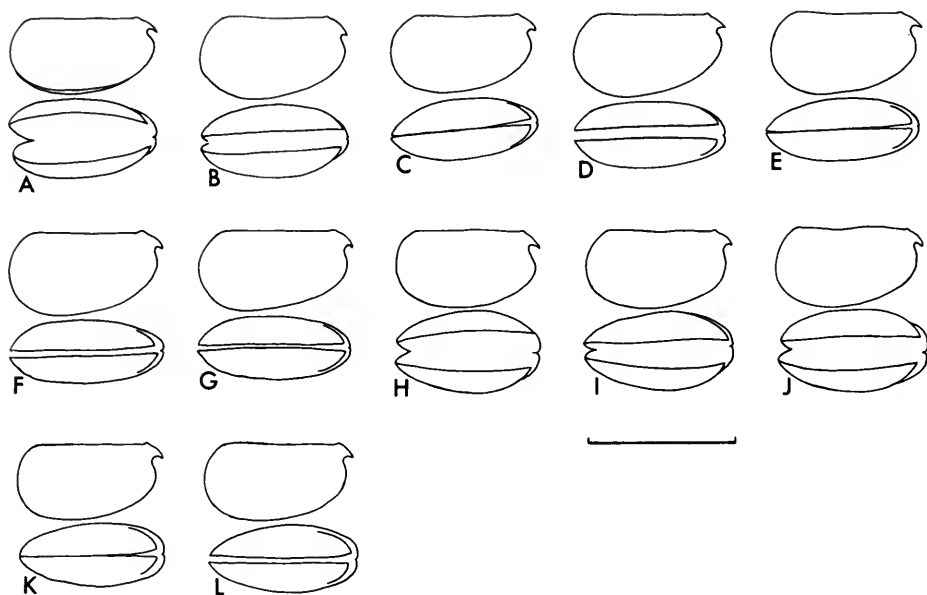
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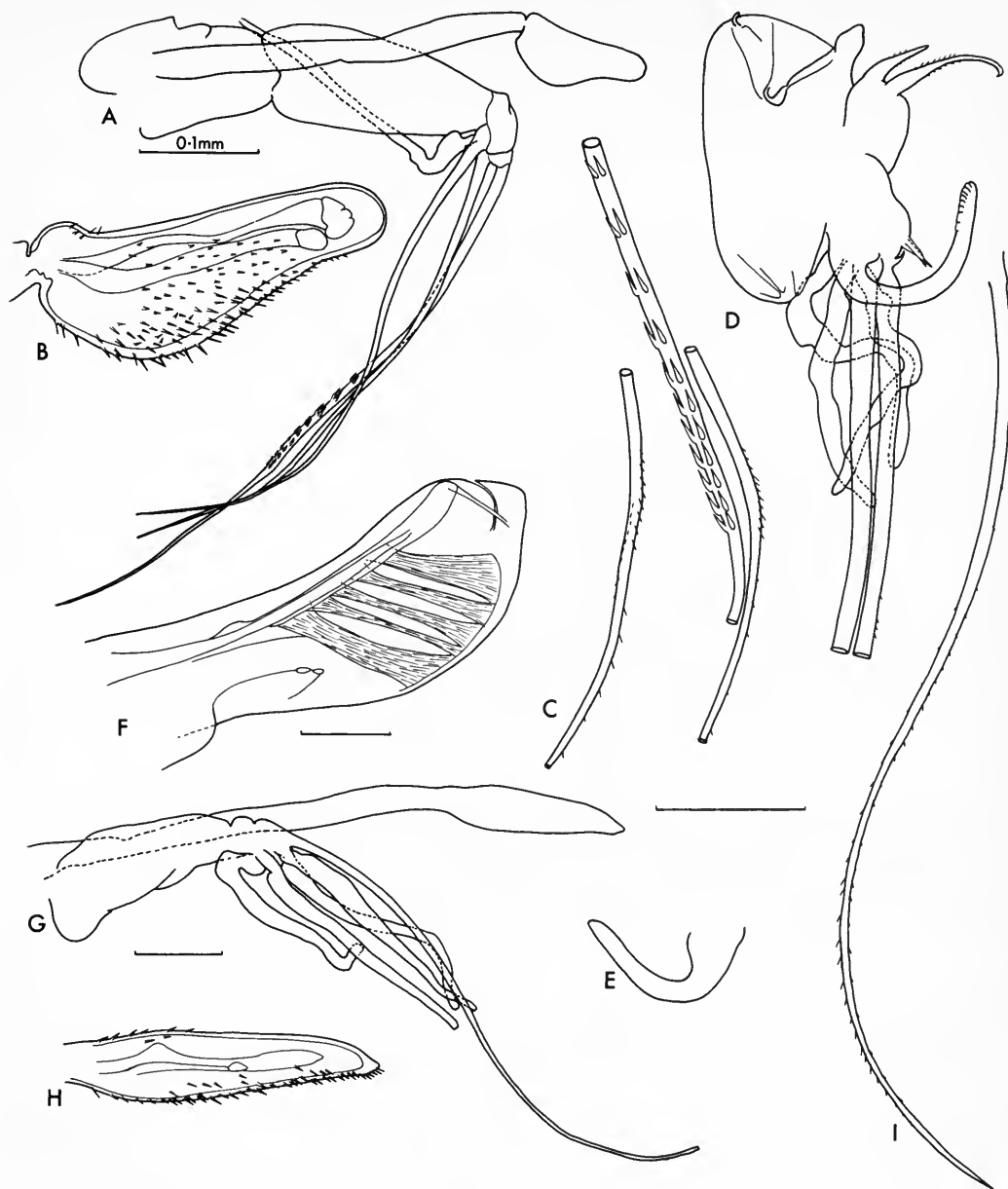
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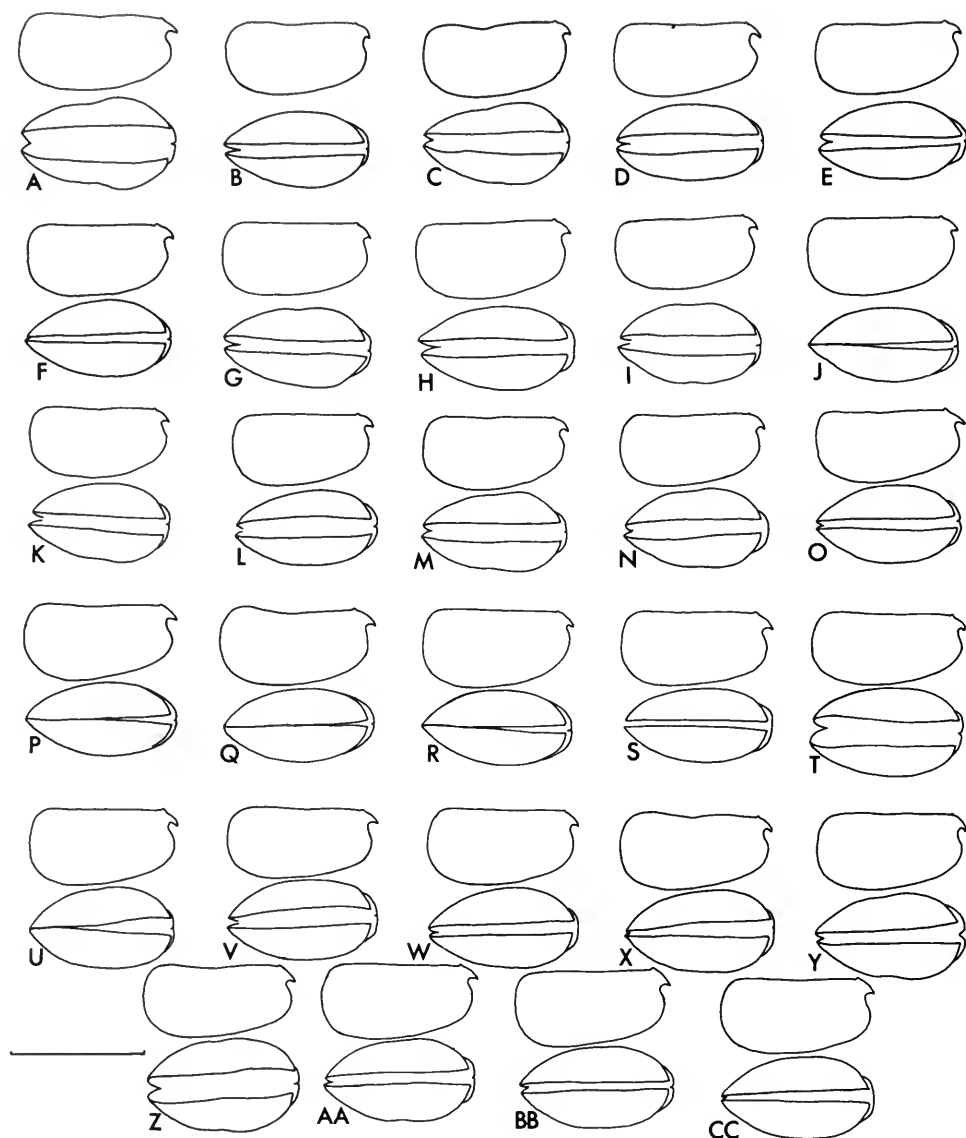
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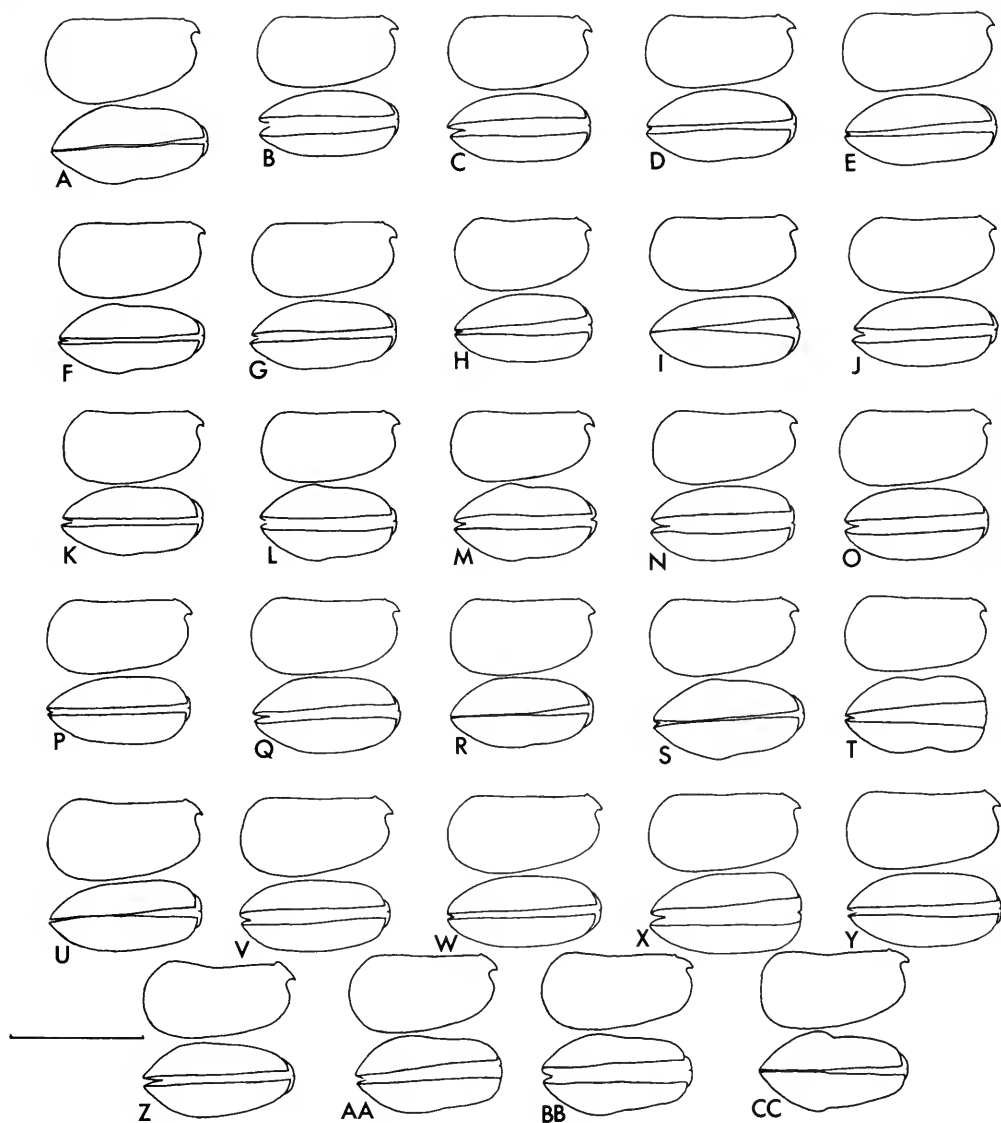
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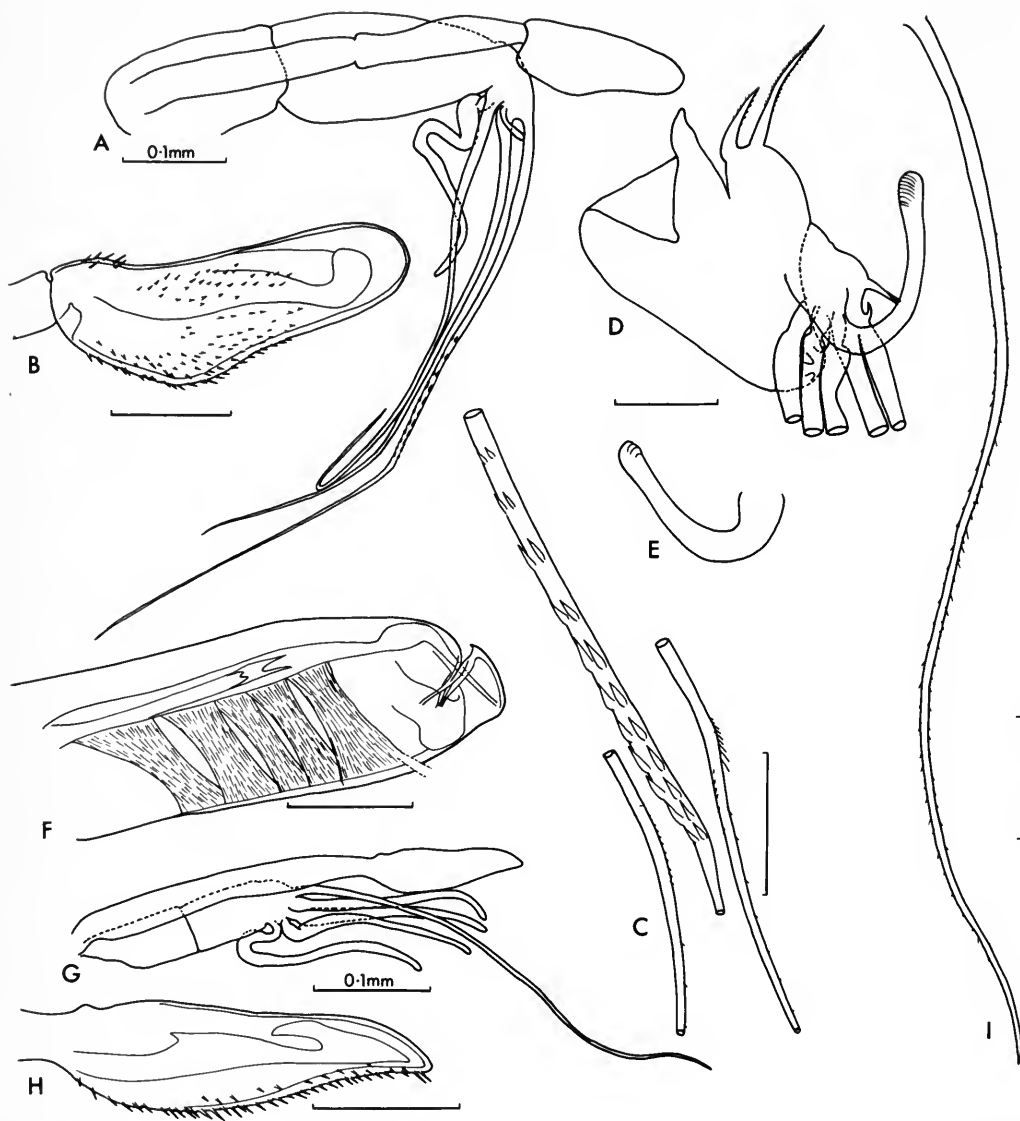
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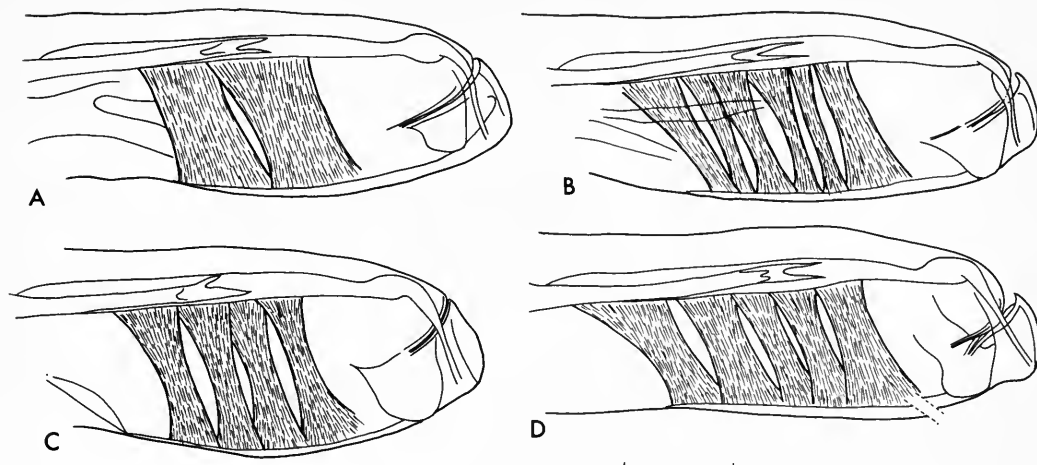
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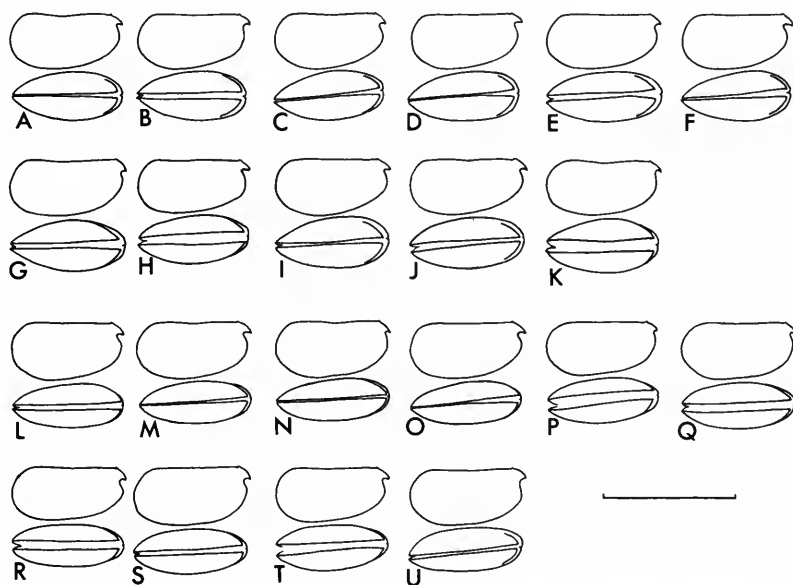
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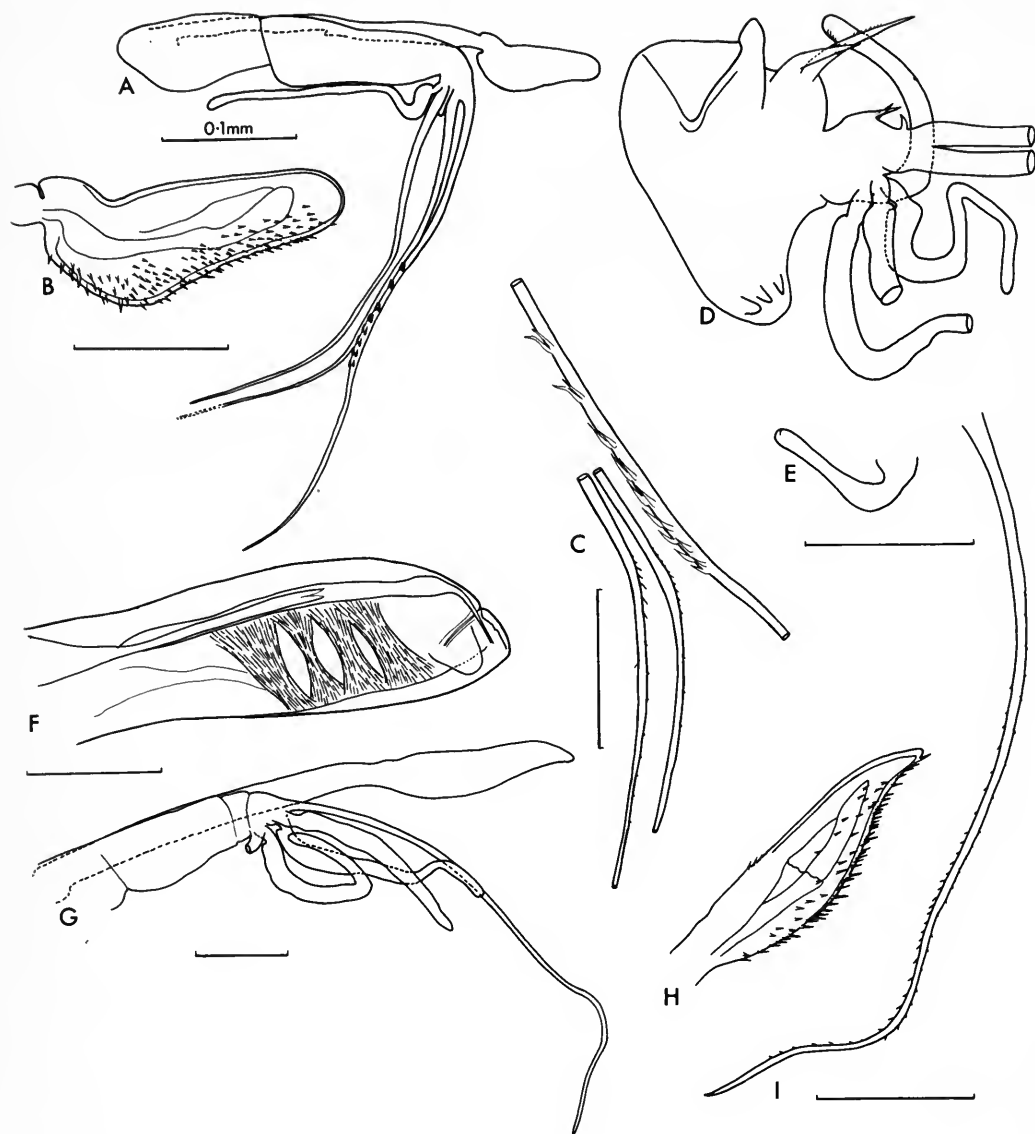
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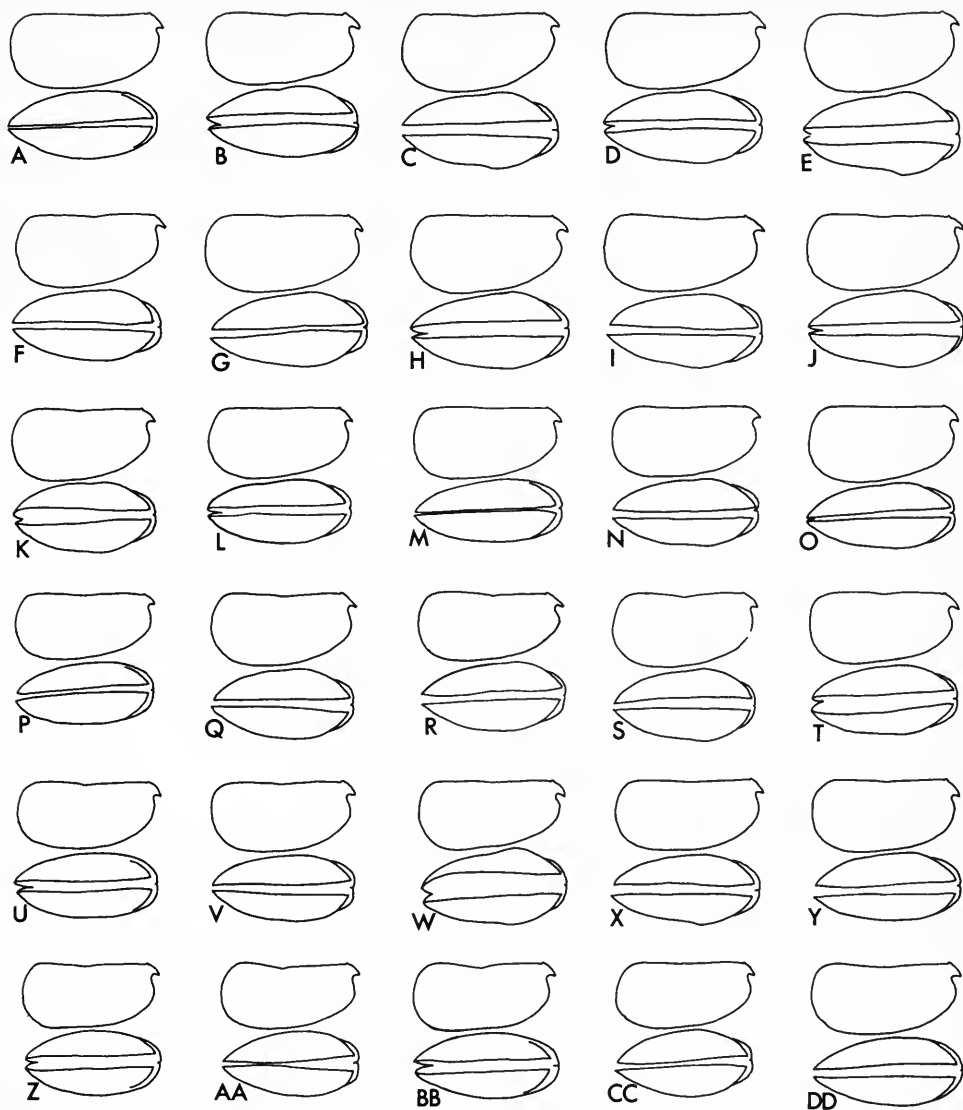
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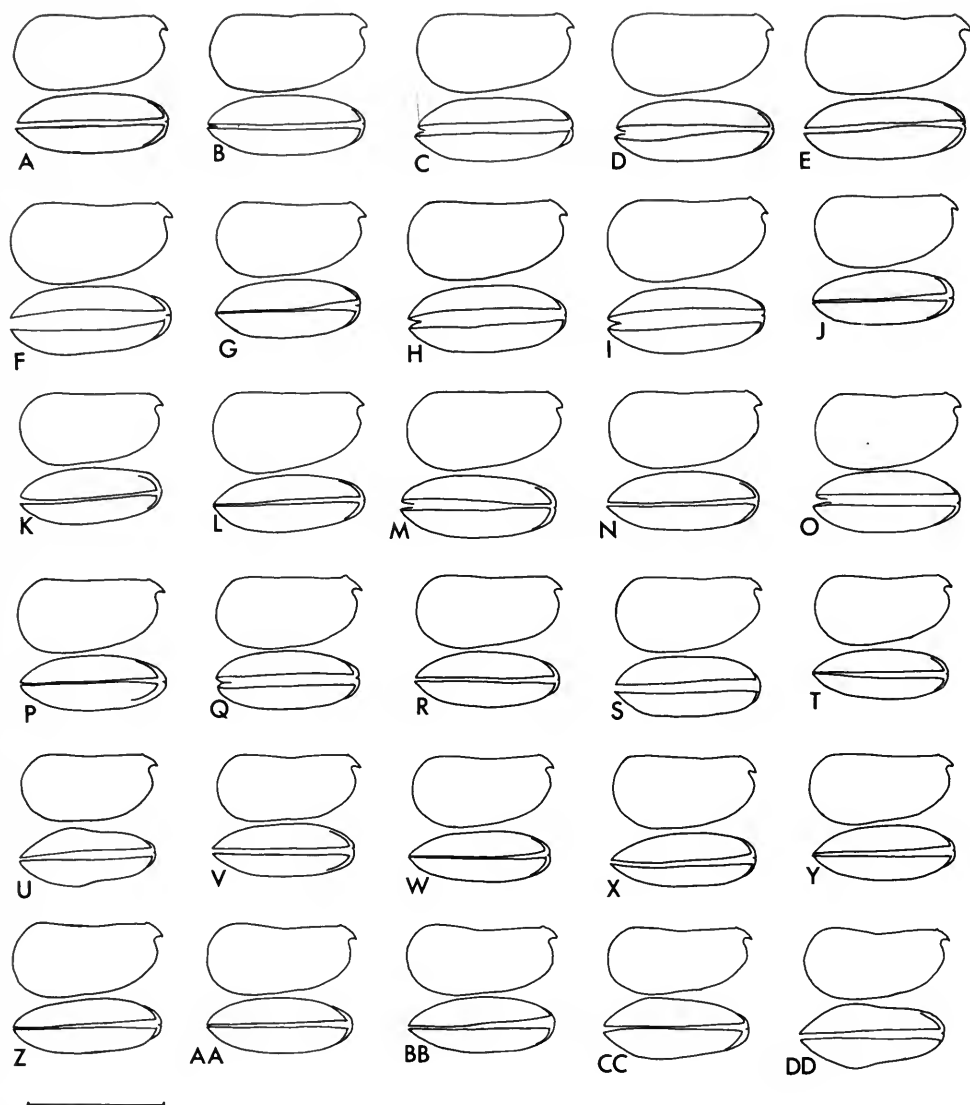
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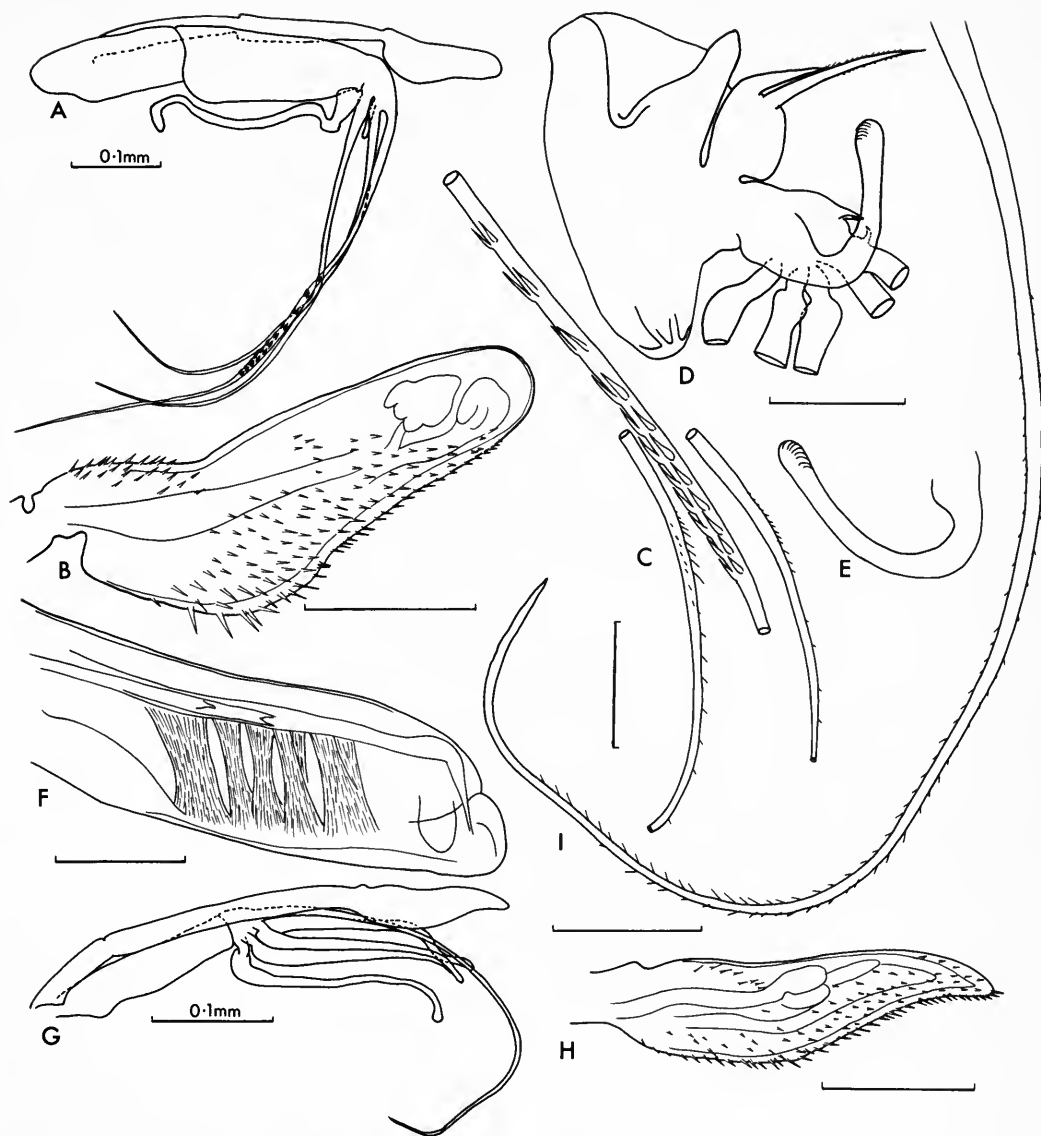
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Introduction

The Edible Crab, *Cancer pagurus* Linnaeus occurs from northern Norway (Christiansen, 1969 : 43) to Portugal (Nobre, 1936 : 50); its presence in the Mediterranean requires confirmation (see Zariquiey Alvarez, 1968 : 345–7). In British coastal waters *C. pagurus* is the object of local but important fisheries and in recent years has been subjected to special studies resulting in a greater understanding of its bionomics (see Edwards, 1978). By comparison, the larval development of *C. pagurus* is not well documented. There are several accounts of the first zoeal stage (see below) of *C. pagurus* but the complete larval development has been described superficially by only Lebour (1928), the early stages from laboratory reared material and the later ones from plankton caught specimens.

In 1979 *C. pagurus* was successfully reared to third crab stage in the BM(NH) and from this material the first account of the complete laboratory larval development of this species is now given.

Materials and methods

The female crab from which the larvae were reared was collected off Shoalstone Point, Devon (SX937568) from a depth of 15 m at a bottom temperature of 10°C in June 1979. The specimen was presented to this Museum by Alan Howard, Fisheries Laboratory MAFF, Burnham-on-Crouch, Essex. The larvae were reared using methods described by Rice & Ingle (1975) and Ingle & Clark (1977). All material was fixed and stored in the preservative formulated by Steedman (1976 : 148) and later transferred to 70% ethanol alcohol. Drawings and meaurements were made with the aid of a *camera lucida*. Measurements are as follows: T.T. = total lengths of zoeae measured between tips of dorsal and rostral spines; C.L. = carapace lengths measured from between eyes to posteriolateral carapace margin for zoeae, from rostral tip (for megalopa) and frontal margin (for crab stages) to median posterior carapace margin; the C.W. (= carapace width) of crab stages was taken at the widest part of the carapace.

The female and reared material are deposited in the Collections of the Zoology Department, British Museum (Natural History) registration number 1980 : 121–122.

Descriptions

Cancer pagurus Linnaeus, 1758

Cancer pagurus Thompson, 1828 : Pl. VIII, fig. 1 (1st zoea); Cunningham, 1898 : Pl. 21, figs 1–2 (1st, 2nd crab); Williamson, 1900 : Pl. 1, fig. 4 (1st zoea); 1904 : Pl. 4, figs 71–81 (11 crab stages); Pearson, 1908 : 460, Pl. 13, figs 83–87 (prezoea, 1st zoea); Nordgaard, 1911 : 39, figs 1,2 (1st zoea); Williamson, 1911 : 17, Pl. 4, figs 50–67 (prezoea, 1st zoea); 1915 : 485, figs 307–310 (1st zoea, 1st

crab); Lebour, 1928 : 522, figs 2 (11–15), 4 (22–23), Pl. 1, fig. 10, Pl. 5, fig. 5, Pl. 10, figs 3–5 (1st–5th zoeae, megal., 1st–4th crab); Gurney, 1942 : fig. 38A (5th zoea), fig. 42A (2nd or 3rd zoea); Rice, 1975 : 237, fig. 1 (1st zoea).

FIRST ZOEA

Dimensions: T.T. 2·5 mm, C.L. 0·6 mm.

Carapace (Fig. 1a): Dorsal spine long, narrowing distally and slightly curved backwards; rostral spine thin, slightly sinuous, slightly shorter than dorsal spine and minutely spinulate; lateral spines long about $\frac{1}{2}$ carapace length; dorso-median elevation prominent; a pair of anterio-median and posterio-dorsal setae; posterior margin with 6 short setae.

Eyes: Partly fused to carapace.

Antennule Fig. 2f): Unsegmented, with 3 terminal aesthetascs and one short seta.

Antenna (Fig. 2a): Spinous process about $3\frac{1}{2}$ × length of exopod, distal $\frac{1}{2}$ spinulate; exopod with one terminal spine and 2 setae.

Mandible (Fig. 3a): Incisor and molar processes well developed, palp absent.

Maxillule (Fig. 3d): Endopod 2-segmented with 1,6 setae; basal endite with 5 setae-spines, coxal with 7 setae-spines.

Maxilla (Fig. 4b): Endopod with large outer and smaller inner lobe with 5 + 3 setae; basal endite with large outer and smaller inner lobe, with 4 + 5 setae; coxal endite with large outer lobe bearing 2 long and one short setae and smaller inner lobe with 3 setae one of which is very long and slightly stouter than others; scaphognathite with 4 marginal setae and a very stout posterior plumose projection.

First maxilliped (Fig. 6a): Basis with 10 setae arranged 2,2,3,3; endopod 5-segmented with 3,2,1,2, 4 + 1 setae; exopod incipiently segmented with 4 terminal plumose setae.

Second maxilliped (Fig. 7a): Basis with 4 setae; endopod 3-segmented with 1,1,4 + 1 setae; exopod with 4 terminal plumose setae.

Third maxilliped: Not developed.

Pereiopods: Not developed

Abdomen (Figs 8a, f): 5-segmented + telson; 2nd segment with pair of dorso-lateral processes; posterio-lateral margins of all segments rounded 3rd–4th with minute spinules. A pair of minute setae near posterio-dorsal margin of segments 2–5. Telson forks long, surfaces minutely spinulate, diverging posteriorly, each with one well developed lateral and one smaller dorsal spine; inner medio-lateral margin of telson with 6 setae, outermost pair with inner margins strongly serrate, median margin of telson strongly convex.

SECOND ZOEA

Dimensions: T.T. 2·8 mm, C.L. 0·8 mm.

Carapace (Fig. 1b): Lateral spines slightly shorter than in first zoea, posterior margin with 9–10 longer setae.

Eyes: Now stalked.

Antennule (Fig. 2g): With 4 aesthetascs and one seta.

Antenna (Fig. 2b): Unchanged.

Mandible: Unchanged.

Maxillule (Fig. 3e): Endopod setation unchanged; outer margin of basal endite with a prominent plumose seta, distal margin with 7 setae-spines; coxal setation unchanged.

Maxilla (Fig. 4c): Endopod, basal and coxal setation unchanged; scaphognathite with 10 plumose setae of equal length.

First maxilliped (Fig. 6b): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.

Second maxilliped (Fig. 7b): Basal and endopod setation unchanged; exopod with 6 terminal plumose setae.

Third maxilliped: Not developed.

Pereiopods: 1–4 present as undifferentiated buds.

Abdomen (Fig. 8b): Posterio-lateral margins of segments 3–4 with incipient acute processes; telson forks longer than in first stage.

THIRD ZOEA

Dimensions: T.T. 3·7 mm, C.L. 1·0 mm.

Carapace (Fig. 1c): With minute setules on dorsal spine; lateral spines slightly smaller than in previous stage.

Eyes: Unchanged.

Antennule (Fig. 2h): With 4 aesthetascs and 2 setae.

Antenna (Fig. 2c): Spinous process slightly less than $3\frac{1}{2} \times$ length of exopod; endopod now developed as a broad bud.

Mandible: Unchanged.

Maxillule (Fig. 3f): Endopod setation unchanged; basal endite with 8–9 setae-spines in some specimens, additional setae very small; coxal setation unchanged.

Maxilla (Fig. 4d): Endopod and basal endite setation unchanged; outer lobe of coxal endite with 4 setae inner lobe unchanged; scaphognathite with 17 setae.

First maxilliped (Fig. 6c): Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.

Second maxilliped (Fig. 7c): Basal and endopod setation unchanged; exopod with 8 terminal plumose setae.

Third maxilliped: Represented as a small bud.

Pereiopods: Buds longer than those of previous stage, 5th pair now present as small buds.

Abdomen (Fig. 8c): 6th segment now present and almost differentiated from telson; spinous process on posterio-lateral margins of segments 3–4 now conspicuous; inner medio-lateral margin of telson with 8 setae. Pleopods represented as small buds on segments 2–5.

FOURTH ZOEA

Dimensions: T.T. 4·3 mm, C.L. 1·2 mm.

Carapace (Fig. 1d): Dorsal and rostral spines slightly stouter than in previous stage and lateral spines smaller; posterior margin of carapace with 11–12 setae.

Eyes: Unchanged.

Antennule (Fig. 2i): Setal formula unchanged but aesthetascs slightly stouter than in previous stage.

Antenna (Fig. 2d): Spinous process less than $3\frac{1}{2} \times$ length of exopod; endopod bud subequal to exopod.

Mandible (Fig. 3b): Outer lip of incisor formed by a prominent row of broad tubercles merging into continuous margin.

Maxillule (Fig. 3g): Endopod setation unchanged; basal endite with 10–11 setae-spines; coxal endite with 8 setae-spines.

Maxilla (Fig. 5a): Endopod setation unchanged; outer lobe of basal endite unchanged, inner lobe with 6 setae; coxal endite unchanged; scaphognathite with 22 setae.

First maxilliped (Fig. 6d): Basal setation unchanged; endopod terminal segment with 6 setae; exopod with 10 distal plumose setae.

Second maxilliped (Fig. 7d): Basal and endopod setation unchanged; exopod with 10 distal plumose setae.

Third maxilliped: Now with a small exopod.

Pereiopods: Longer than in previous stage and incipiently segmented; dactylus differentiated on cheliped.

Abdomen (Figs 8d, g): 6th segment clearly demarcated from telson; posterio-lateral spinous processes on segments 3–5 longer than in previous stage; telson inner medio-lateral margin with 10 setae. Pleopod buds longer than in previous stage.

FIFTH ZOEA

Dimensions: T.T. 4·7 mm., C.L. 1·4 mm.

Carapace (Fig. 1e): Setules on dorsal spine and setae on posterior margin of carapace longer than in previous stage, lateral spine smaller.

Eyes: Unchanged.

Antennule (Fig. 2j): Endopod present as a small bud; exopod with 6 aesthetascs and 4 setae.

Antenna (Fig. 2e): Spinous process × 3 length of exopod; endopod varying from $\frac{1}{2}$ to over $\frac{3}{4}$ length of spinous process and, in some specimens, incipiently segmented.

Mandible (Fig. 3c): Inner margin of incisor process clearly defined as a ridge; mandibular palp present as a small bud.

Maxillule (Fig. 4a): Endopod setation unchanged; basal endite with 13–14 setae-spines; coxal endite with 10 setae-spines.

Maxilla (Fig. 5b): Endopod setation unchanged; outer lobe of basal endite with 6–7 setae, inner with 7 setae; outer lobe of coxal endite unchanged, inner lobe with 3–4 setae; scaphognathite with 31 setae.

First maxilliped (Fig. 6e): Basal and endopod setation unchanged; exopod with 12 distal plumose setae.

Second maxilliped (Fig. 7e): Basal and endopod setation unchanged; exopod with 12 distal plumose setae.

Third maxilliped: Endopod clearly segmented.

Pereiopods: Cheliped well formed, those of 2–5 clearly segmented.

Abdomen (Figs 8e, h): Telson forks less divergent than in previous stages; lateral processes on 2nd segment smaller. Pleopod buds long and now present on 6th segment.

MEGALOPA

Dimensions: C.L. 2·4 mm.

Carapace (Figs 9a, b): Longer than broad, narrowing anteriorly; frontal region (f) with slight median furrow, orbital margin expanded; rostrum long, terminally acute and horizontally directed, hepatic regions (h) inflated, protogastric (p) each with a raised carina, epibranchial (e) and mesobranchial (m) regions defined by a carina, cardiac region with a long posteriorly directed horizontal spine.

Eyes: Large, elongated.

Antennule (Fig. 10a): Peduncle indistinctly 3-segmented, 2nd segment with 1–2 short setae; exopod 4-segmented, 2nd with 8 and 3rd with 4 aesthetascs and 1 seta, 4th with 1 terminal and 1 subterminal seta; endopod with 4 terminal and 1 subterminal setae.

Antenna (Fig. 10b): Peduncle with 3 segments; flagellum 6-segmented, setal formula (from distal to proximal) 4,3,0,4,3,0,2,1,1,1.

Mandible (Fig. 10c): Molar and incisor parts not distinguishable one from the other, disto-internal angle acutely produced; mandibular palp 3-segmented, terminal segment longest with 7 distal setae.

Maxillule (Fig. 10d): Endopod now unsegmented and with 4 setae; basal endite with 21 setae-spines; coxal endite with 13–14 setae.

Maxilla (Fig. 10e): Endopod now reduced to acute lobe, unarmed; basal endite with 8 + 9 setae, with 3–4, 5 setae; scaphognathite with 48–49 plumose setae shorter than in last zoeal stage.

First maxilliped (Fig. 11a): Coxal segment partly differentiated from basis and with 11–12 setae on inner margin, basis with 19–22 setae; endopod unsegmented with 4 setae on outer margin and 4 apical setae; exopod 2-segmented, proximal with 2 disto-external setae and terminal segment with 4 apical setae; epipod well developed and with 4–5 setae.

Second maxilliped (Fig. 11b): Coxal and basal segments undifferentiated with 0–2 setae on inner margin; endopod carpus (antipenultimate segment) with 1 disto-internal seta, propodus with 5 disto-external setae, dactylus with 5 spines and 5 setae; exopod 2-segmented, terminal segment with 4 long setae; epipod short and broad.

Third maxilliped (Fig. 11c): Basis with 2 setae on internal margin and differentiated from coxa; endopod, ischium with 3–4 setae on outer surface and 13–14 setae placed on or near inner margin that also bears acute tubercles, merus with 2–3 outer disto-external setae and 3 setae on internal margin, carpus with 1 disto-external and 3 disto-internal setae, propodus with 2 disto-external setae and 4 setae on internal margin, dactylus with 7 setae; exopod 2-segmented, distal segment with 4 setae; epipod bifurcate, longest branch with 13–14 setae that extend onto coxal surface.

Pereiopods (Figs 12 a–e): Cheliped stout, with a prominent ischial spine, inner distal propodal margin with 4 blunt teeth, inner dactylar margin with at least 2 indistinct teeth. Pereiopods 2–5 relatively stout, coxa of 2nd (Fig. 12b) with acute process, dactylus of 5th pereiopod with 3 long terminal setae.

Abdomen (Figs 9a,c,d, 12h): With 6 segments + telson; posterio-lateral margins of 2nd–5th broadly truncate and 3rd–5th minutely spinose; a small pair of dorso-median setae present near posterior margins of segments 2–6 along with other setae as shown. Telson (Fig. 12h) broader than long, with three pairs of dorso-median setae and a pair of setae on posterior margin. Five pairs of pleopods, distal segment of pleopod exopods with long plumose marginal setae, 1st (Fig. 12f) with 16, 2nd 15–16, 3rd 15–17, 4th (Fig. 12g) and 5th (uropods, Fig. 12h) with 8 setae respectively, endopods of pleopods 1–4 with 3 distally placed coupling hooks on internal margins.

First crab

Dimensions: C.L. 2·3 mm., C.W. 2·4 mm.

Carapace (Fig. 13a): Maximum width at about 4th pair of anterio-lateral teeth. Dorsal surface minutely denticulate, protogastric and meso-metabranchial regions slightly inflated and with long setae; frontal and orbital margins irregularly denticulate; anterio-lateral margin setose, with 4 large bi- or tridentate teeth with additional spines between them; posterio-lateral and posterior margin of carapace setose. Eyestalks with 2–3 spines.

Second crab

Dimensions: C.L. 2·9mm., C.W. 3·9 mm.

Carapace (Fig. 13b): Maximum width now at about 7th anterio-lateral tooth. Denticles smaller than in 1st stage and marginal setae almost wholly absent; anterio-lateral margins with 8–9 spinose teeth.

Third crab

Dimensions: C.L. 3·7 mm., C.W. 4·9 mm.

Carapace (Fig. 13c): Denticles now very small; anterio-lateral margins now with 9 defined, obtusely serrate teeth and one posterio-lateral tooth. Spines on eyestalks reduced.

Variation

The material reared for this present study agrees with previously published accounts of *C. pagurus* larvae except for the minor details listed in Table 1 in which the various available descriptions of the 1st zoeal stage are compared. In addition, Lebour (1928 : 523) described the fourth zoea as having 'two pairs of extra internal spines to telson' compared with one extra pair acquired at this stage by the present specimens. Gurney (1942, figs 38A & 42A) figured the maxillule and 1st–3rd maxillipeds of *C. pagurus*. His figure of the maxillule can be attributed to the fifth stage zoea but lacks a seta on the first segment of the endopod whilst the basis of the first maxilliped (perhaps of a 2nd or 3rd stage) has only three setae and an endopod setal formula of 0,2,1,2,2, on the first and 1 + 4 on the second and with the exopods of both pairs with 7 terminal setae.

Samples of *C. pagurus* zoeae collected in the southern N. Sea, at 53°50′N: 1°00′E from 6–17 July 1976, were compared with the present laboratory reared material. Stages IV and V of the N. Sea samples were found to be considerably larger (i.e. T.T. ZIV 4·7 mm; ZV 5·6 mm) than the reared specimens (i.e. ZIV 4·3 mm; ZV 4·7 mm) and a small percentage of the first zoeae of the plankton specimens was found to have one or both telson forks bifurcated and, in some, an extra medio-lateral telson spine was present as shown in Fig. 13e. In this figured specimen the lateral spine on the right fork of the telson and the small lateral and dorsal spine are absent; an extra small spinule is developed on the left outer bifurcation

and the seta on the basal segment of the maxillule endopod is also bifurcated. It is not known if these abnormalities are of genotypic or phenotypic origin.

Distinguishing features of *C. pagurus* larvae

From the present larval account of *C. pagurus* it may now be possible to distinguish the zoeae of this species from the early zoeal stages described of many other brachyrhynch crabs that occur in British coastal waters using the following combined features. (1) In *C. pagurus* only the second segment of the abdomen is armed with a pair of dorso-lateral processes. Early zoeal stages of *Polybius henslowii* Leach, *Bathynectes longipes* (Risso), *Liocarcinus* (= *Macropipus*) *spp., Goneplax rhomboides* (Linnaeus), *Geryon tridens* Kroyer, *Pilumnus hirtellus* (Linnaeus), *Xantho incisus* Leach, *Monodaeus couchi* (Couch), *Pinnotheres pisum* (Linnaeus) and *P. pinnotheres* (Linnaeus) have dorso-lateral processes on more than one segment. (2) *C. pagurus* has lateral spines on the carapace; these are absent in zoeae of *C. maenas* (Linnaeus) and *Portumnus latipes* (Pennant). (3) *C. pagurus* zoeae have two dorso-lateral spines on each telson fork; the zoeae of *Corystes cassivelaunus* (Pennant) and *Thia scutellata* (Fabricius) have only one spine. (4) *C. pagurus* zoeae have smooth posterio-lateral margins to the abdominal segments except in the first zoeal stage when these margins may have a few very minute spinules. The zoeae of *Pirimela denticulata* has conspicuously denticulate posterio-lateral margins. (5) In *C. pagurus* the outer pair of telson mesio-lateral spines have strongly serrate outer margins. By comparison these serrations are far less developed in zoeae examined belonging to *Liocarcinus spp., C. maenas, X. incisus, M. couchii, P. hirtellus* and *G. tridens.*

Zoeae of *C. pagurus* are separated less satisfactorily from those of *Atelecyclus rotundatus* (Olivi) by having a relatively straight dorsal spine on the carapace, three distal 'setae' on the antennal exopod and 1,6 setae respectively on the endopod segments of the maxillule. Lebour (1928 : 524, fig. 4, 1–5, 26) described the zoeae of *A. rotundatus* as having a curved dorsal carapace spine in the early stages, two distal setae on the antennal exopod and 1,4 setae on the respective segments of the maxillule endopod. Rice (1980 : 336) has included the following two characters in his larval diagnosis of the subfamily Atelecyclinae (to which *A. rotundatus* belongs). (a) A maxillule endopod with 1,6 setae; (b) the diminutive size of the middle seta of the distal two groups of three on the first maxilliped basis. These two subfamilial features are based entirely upon the zoeal descriptions of *Erimacrus* and *Telmessus* and their confirmation in larvae belonging to *Atelecyclus* will have to await further laboratory rearing and descriptions of larvae belonging to this genus, particularly of *A. rotundatus,* to establish the features for separating *Atelecyclus* larvae from those of *C. pagurus.*

An additional feature that may prove of value for separating the early zoeal stages of *C. pagurus* from corresponding stages of other species is the exceedingly long spine on the inner lobe of the coxa of the maxilla (see Fig. 13e). A spine of this proportion is depicted for *C. magister* Dana by Poole (1966, fig. 1g). This corresponding spine on the coxa of the maxilla of zoeae I,II of *C. maenas, Liocarcinus spp., G. tridens, X. incisus* and *M. couchi* never overreaches the other coxal spines as seen in *C. pagurus* (cf. figs 13 d & e).

The megalopa of *C. pagurus* has a prominent cardiac spine on the carapace that separates it from megalopae of *Liocarcinus spp., P. henslowii, C. maenas, Xaiva biguttata* (Risso), *T. scutellata, P. denticulata, G. tridens, G. rhomboides, P. hirtellus, X. incisus, M. couchi* and *Pinnotheres spp.* The narrow styliform dactylus of the 5th pereiopod and the presence of 8 uropodal setae distinguishes the megalopa of *C. pagurus* from that of *P. latipes* in which the 5th pereiopod dactylus is lanceolate, the uropods have only 7 setae and the dorsal spine on the carapace arises from the meta- or urogastric regions and is thus further forward than in *C. pagurus* (see Lebour, 1944: fig. 3 d). The absence of spines on the submedian and hepatic regions of the carapace and the presence of 3 setae on the dactylus of the 5th pereiopod separate the megalopa of *C. pagurus* from that of *C. cassivelaunus*; the latter species has

submedian and hepatic spines (as well as a pair of minute protogastric spinules) and the 5th pereiopod dactylus has only 2 setae (see Ingle & Rice, 1971: figs 7F & 8).

Further studies are required to establish satisfactory features for separating the megalopa of *C. pagurus* from that of *A. rotundatus*. Lebour (1928 : 525, Pl. IX, fig. 5) states that the megalopa of *A. rotundatus* has 10–11 uropodal setae (*C. pagurus* has 8 setae), and depicts 4–5 setae on the 5th pereiopod dactylus (*C. pagurus* has only 3 setae).

Comparisons of larvae of the species of *Cancer*

The first zoeal stage of eleven and the complete larval development of eight species of *Cancer* have been described. The majority of these accounts omit details of features such as carapace setation of the zoeae, lateral spines of the telson, the armature of the megalopal carapace, proximal segments of the pereiopods and setation of the telson. Distinctive larval features described in these various accounts are summarized in Tables 2–4. No single character (except perhaps the exceedingly large size and exceptionally large number of setae on the antennule and scaphognathite in later stages of *C. magister* and the presumably 5-segmented abdomen described for all stages of this species (see Poole, 1966)) can be used to separate the known species of *Cancer* larvae, but they appear to be identifiable on combined features. A comparison of the first zoeal stages of Pacific and Atlantic species of *Cancer* suggest that those from the former region have more pronounced posterio-lateral spines on the abdominal segments and a tendency to fewer antennular aesthetascs-setae. Zoo-geographic differences are more obvious when the fifth zoeal stages are compared. Pacific species have a maximum of 6 setae on the maxilla endopod; this number is always 8 in Atlantic species except for *C. ? bellianus* that has 7 setae. There are never more than 9 setae on the 1st maxilliped basis in Pacific zoeae compared with 10 or more in Atlantic ones.

Rice (1975 & 1980 : 331) recognized trends towards the existence of two possible groups of *Cancer* zoeae with respect to the armature of appendages: (a) species with 2 setae on the basal segment of the endopod of the first maxilliped, the maxillule endopod segments armed with 1,5 setae respectively and the endopod of the maxilla with 6 setae; (b) species with 3 setae on the basal segment of the endopod, 1,6 setae on the maxillule endopod and the endopod of the maxilla armed with 7–8 setae. This present study also suggests that zoeae attributable to group (a) have only 2 and those in group (b) 3 terminal 'spines' on the antennal exopod. Zoeae in which the above mentioned features are not combined are *C. amphioetus, C. gibbosulus, C. porteri* and zoea V of *C. ? bellianus*.

Acknowledgements

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Table 1 Comparative features of first zoeal stage of *Cancer pagurus* after various authors and compared with the present material

Features	Williamson 1900 : 1911	Pearson 1908	Norgaard 1911	Lebour 1928	Rice 1975	Present material
Length of dorsal to rostral spine:	slightly longer	much shorter	longer distally	equal to	longer	slightly longer
Spinulation of dorsal spine:	well developed	not shown	not shown	not shown	absent	absent
Spinulation of rostral spine:	well developed	not shown		not shown	minute	minute
Setae + aesthetascs on antennule:	5	4	?	?	3–4	4
Antennal spinous process to rostral length:	much more than half	about half	slightly less than half	?	less than half	slightly more than half
Antennal exopod to spinous process length:	slightly less than half	about one third	about one third	about one third	slightly less than one third	slightly less than one third
Maxillule, spines-setae on coxa:	7	–	–	6	–	7
Maxilla, spines-setae on endopod outer lobe:	5 + one minute seta	–	–	4	5 (or 4)	5
Maxilla, spines-setae on coxal endite:	6 ? + 3	–	–	total of 5	3 + 3	3 + 3
Second maxilliped, setae on basis:	3	–	–	–	4	4
Second maxilliped, endopod setae:	0,1,5 + 1	–	–	–	1,1,5 + 1	1,1,4 + 1
Abdominal segments, spinules on posterio-lateral margins:	present on 2–5	not shown	not shown	not shown	not shown	present on 3–4

Table 2 Comparative features of first zoeal stages of eleven *Cancer* species after: 1 Present material & Rice 1975: 2 Connolly 1923: 3 Sastry 1977*a*: 4 Sastry 1977*b*: 5 Fagetti Guaita 1960: 6 Aikawa 1937: 7 Mir 1961: 8 Poole 1966: 9 Roesijadi 1976: 10 Trask 1974: 11 Anderson 1978: 12 Rice 1975: 13 Trask 1970: 14 Ally 1975: 15 Iwata 1973. $\leqslant$ = slightly or much less than . $\geqslant$ = slightly greater or equal to, * = approx. lengths calculated from illustrations

	ATLANTIC			PACIFIC							
Authors:	*C. pagurus* 1	*C. irroratus* 2,3	*C. borealis* 4	*C. porteri* 5	*C. gibbosulus* 6	*C. magister* 7,8	*C. antennarius* 7,9	*C. anthonyi* 10,11,12	*C. productus* 13	*C. gracilis* 14	*C. amphioetus* 15
Dorsal spine/Carapace length:	$\geqslant \times 2$	$\geqslant \times 1\frac{1}{2}$	$\geqslant \times 1$	$\geqslant \times 1\frac{1}{2}$	$\times 1\frac{1}{2}$	$\leqslant \times 1\frac{1}{2}$	$\geqslant \times 1$	$\geqslant \times 1$	$\geqslant \times 1$	$\geqslant \times 1$	$\leqslant \times 1\frac{1}{2}$
Antennule, aesthetascs-setae:	4	5² 4³	4	4	?	3	3-4	3	3	5	3
Antenna, exopod distal spines:	3	3	3	3	2	3	2	2	3	2	2
Maxillule, endopod setae:	1,6	1,6	1,6	1,5	1,6	1,6	1,4	1,5	1,6	1,5	1,6
Maxillule, basis; coxa, setae-spines:	5,7	5,7	5,6	5,4	5,7	5,6	5,6	5,6	5,6	5,7	5,6
Maxilla, endopod; basis; coxa, setae-spines:	5+3,4+3, 3+3	4+3,3+5 ?3+3² 5+3 4+5, 4+3³	5+3,4+5, 3+3	4+3,4+4, 3+3	3+3,4+4, 3+3	4+3,4+5, 4+3	3+3,4+5, 5⁷ or 3+3⁹	4+2,4+4, 3+3⁷ 6,3+3,3+3¹⁰ 3+3,4+4, 3+3¹¹	4+3,4+5 4+3	3+3,4+5, 3+3	3+3,4+4, 3+4
Maxilla scaphognathite:	4+1	4+1	4+1	4+1	4+1	3+1	3+1	4+1	4+1	4+1	4+?1
First maxilliped basis, setae:	10	5² 9³	9	9	?	9	9	8	10	9	8
First maxilliped endopod setae:	3,2,1,2, 4+1	3,2,1,2, 4+1	3,2,1,2, 4+1	3,2,1,2, 4+1		3,2,1,2, 4+1	2,2,1,2, 4+1	2,2,1,2, 4+1	3,2,1,2, 4+1	2,2,1,2, 4+1	2,2,2,2, 4+1
Abdominal segments, posterio-lateral margins:	3-4 obtuse minutely spinulate	2-4 obtuse³	1-5 obtuse	3-5 spinose	4-5 slightly spinose	1-5 spinose	3-5 slightly spinose	3-5¹⁰ slightly spinose 1-5¹¹ slightly spinose	1-5 slightly spinose	2-5 slightly spinose	3-5 obtuse
Length*, carapace vertex to telson tips:	1·8 mm	1·5 mm	1·2 mm	1·5 mm	1·4 mm	2·5 mm	1·3 mm	1·2 mm	1·8 mm	1·2 mm	1·7 mm

Table 3 Comparative features of fifth zoeal stages of nine *Cancer* species. *See legend to Table 2 otherwise 1 Frost 1936: 2 Rice & Williamson 1977

	ATLANTIC				PACIFIC				
*Authors:	*C. pagurus*[1]	*C. irroratus*[1]	*C. borealis*	*C. ?bellianus*[2]	*C. magister*	*C. antennarius*	*C. anthonyi*	*C. productus*	*C. gracilis*
Dorsal spine/carapace length: Antennule, aesthetascs-setae:	⩾ × 1¼ 10	⩽ × 1 25	⩾ × 1 13	⩾ × 1 11	⩾ × 1¼ 29	⩾ × 1 14	⩾ × 1 20[10] 17[11]	⩾ × 1 24	⩾ × 1 25–26
Antenna, exopod distal spines:	3	3	3	broken	3	2	2	3	2
Maxillule, endopod setae:	1,6	1,6	1,6	1,5	1,6	1,5	1,5	1,6	1,5
Maxillule, basis; coxa, setae-spines:	14,10	18,10	12,10	not described	21–23,16	14,7	16,11[10] 15,10[11]	17,10	15,10
Maxilla, endopod; basis; coxa setae-spines:	5 + 3,7 + 7, 4 + 4	5 + 3,10 + 8, 5 + 5	5 + 3,7 + 7, 4 + 3	endopod 3 + 4 basis, coxa not described	4 + 3,14 + 12, 5 + 5	3 + 3,8 + 8, 3 + 3	3 + 3,8 + 7[10] 4 + 4 3 + 3,7 + 8[11], 4 + 4	4 + 3,8 + 8, 4 + 4	3 + 3,7 + 7 or 7 + 8, 4 + 4
Maxilla scaphognathite setae:	31	37–38	29	36–37	49–50	34–35	34–36[10] 32–36[11]	37–38	33–36
First maxilliped basis, setae:	10	12	10	10	9	9	3[10] 8[11]	8	9
First maxilliped endopod, setae:	3,2,1,2, 5 + 1	3,2,1,2, 5 + 1	3,2,1,2, 5 + 1	3,2,1,2, 5 + 1	3,2,1,2, 5 + 1	2,2,1,2, 5 + 1	2,2,1,2, 4 + 1[10] 2,2,1,2, 5 + 1[11]	3,2,1,2, 5 + 1	2,2,1,2, 5 + 1
Second maxilliped basis, setae:	4	3	5	4	4	4	4	4	4
Second maxilliped endopod, setae:	1,1,4 + 1	1,1,6 + 1	1,1,4 + 1	1,1,4 + 1	1,1,4 + 1	1,1,1,4 + 1 4 segmented	1,1,6 + 1[10] 1,1,4 + 1[11]	1,1,4 + 1	1,1,4 + 1
Abdominal segments:	6	6	6	6	5	6	6	5	6
Abdominal segments spinosed postero-lateral margins:	3–5	3–5	2–5	3–5	2 (minute) 3–5	3–5	3–4[10] 1–6[11]	3–5	2 (minute) 3–4
Length, carapace vertex to telson tips:	4·4 mm	3·2 mm	4·2 mm	5·2 mm	9·0 mm	4·0 mm	3·1 mm	4·0 mm	3·3 mm

Table 4 Comparative features of megalopae of eight *Cancer* species after various authors in Table 2

	C. pagurus	C. irroratus	C. borealis	C. magister	C. antennarius	C. anthonyi	C. productus	C. gracilis
Antennule exopod, aesthetascs-setae:	15	26	22	41	20	22–27[10] 32[11]	30	34
Antennule endopod, setae:	4	6	4	9	5	5[10] 7[11]	5	6
Antenna segments: Antennal setae, proximal to distal:	10 4,3,0,4,3,0, 2,1,1,1	10 4,4,6,0,3 0,4,2,2,0	11 5,4,0,3,0, 5,0,0,3,1,0	12 5,5,2,6,0, 7,2,0,8,11, 11,0	11 4,4,0,5,0,4, 0,0,4,2,4,	11 4,4,0,4,0,4, 0,0,4,2,2,10 5,5,0,5,0,4, 0,0,3,2,5,[11]	11 5,3,1,3,2,3, 0,0,4,4,5,	10–11 5,4,0–1,5,0,4–3–5, 0,0,4–5,2–3,5
Mandibular palp, setae:	7	9	9	17	9	7[10] 13[11]	12	8
Maxillule endopod, setae:	0,4	1,6	1,5?	0,5	1,5	1,5[10] 1,3[11]	0,4	1,2
Maxillule basis; coxa, setae:	21,14	23,10	14,11	38–43,29–31	17,11	20,8[10] 26–28,16[11]	30–32,15–17	26,14–15
Maxilla scaphognathite, setae:	48–49	46	44–45	110–124	53–55	45–50[10] 47–53[11]	62–64	53–59
Second maxilliped endopod, setae of three distal segments:	1,5,10	2,6,8	1,7,8	6,20,13	0,7,8	0,5,10[10] 1,7,10[11]	0,7,7	1,5–7,8–9
Third maxilliped exopod, setae:	0,4	3,6	0,5	17,10	0,5	0,6[10] 3,6[11]	5,6	2–4,5
Pleopods 1–3 exopod. setae:	16,15–16,15– 17,14–15	15,15,13, 11	16,16,16, 16	32,32,32, 28	19,18,19, 15	16,16,14, 11[10] 16–17,17–18 16–17,15–16[11]	21,19,19. 19	17–19,17–19, 17–18,14–16
Abdominal segments: Uropods exopod, setae:	6 8	6 9	6 10	5 22	6 9	6 7[10] 9–10[11]	5 12	6 7–9
Total lengths:	3·4 mm	3·7 mm	4·2 mm	11 mm	3·8 mm	4·0 mm	6·0 mm	3·2 mm
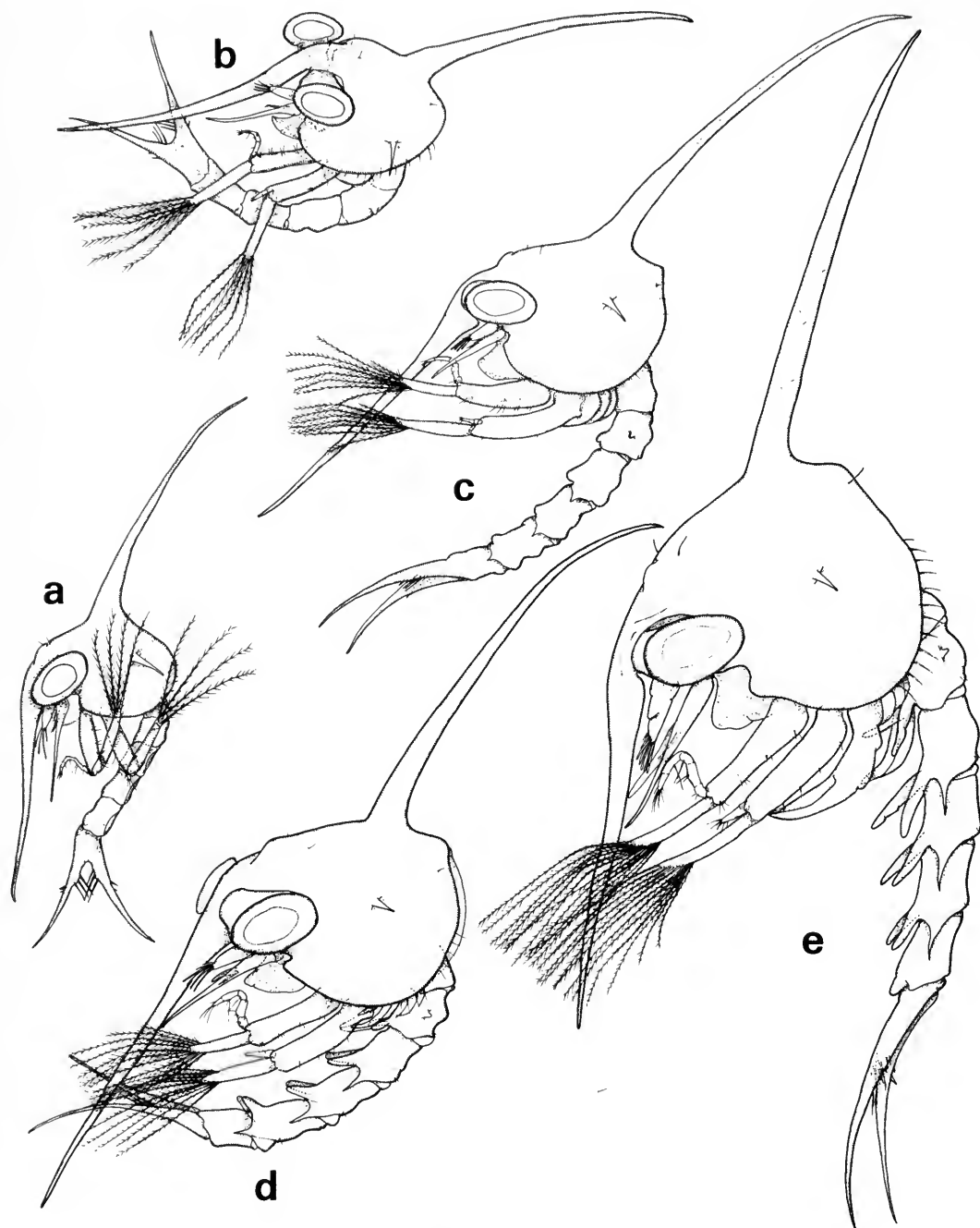
Fig. 1 *Cancer pagurus* L.: a–e 1st–5th zoeae.
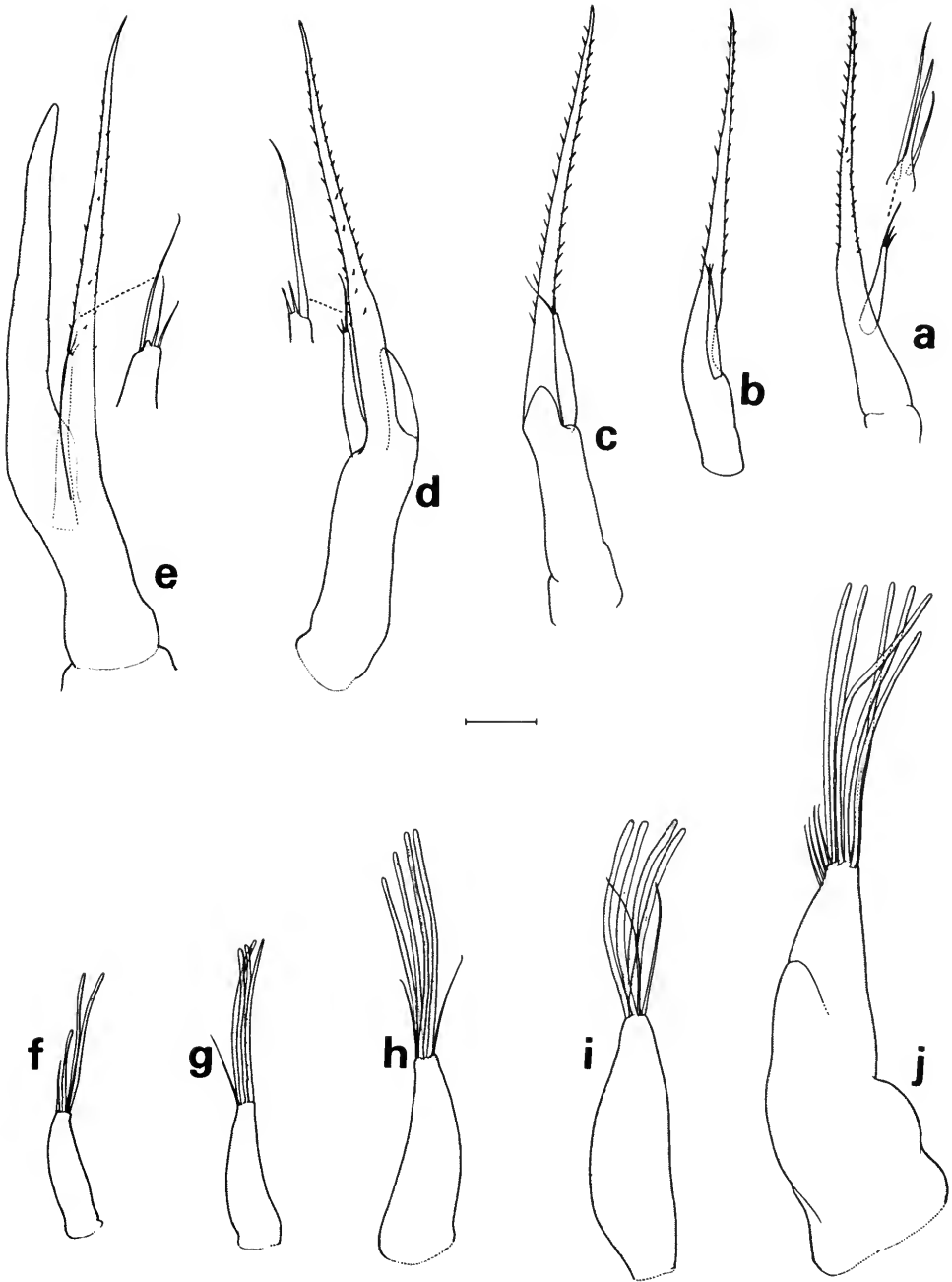
Fig. 2 *Cancer pagurus* L.: a–e antennule; f–j antenna of 1st–5th zoeae; scale = 0·1 mm.
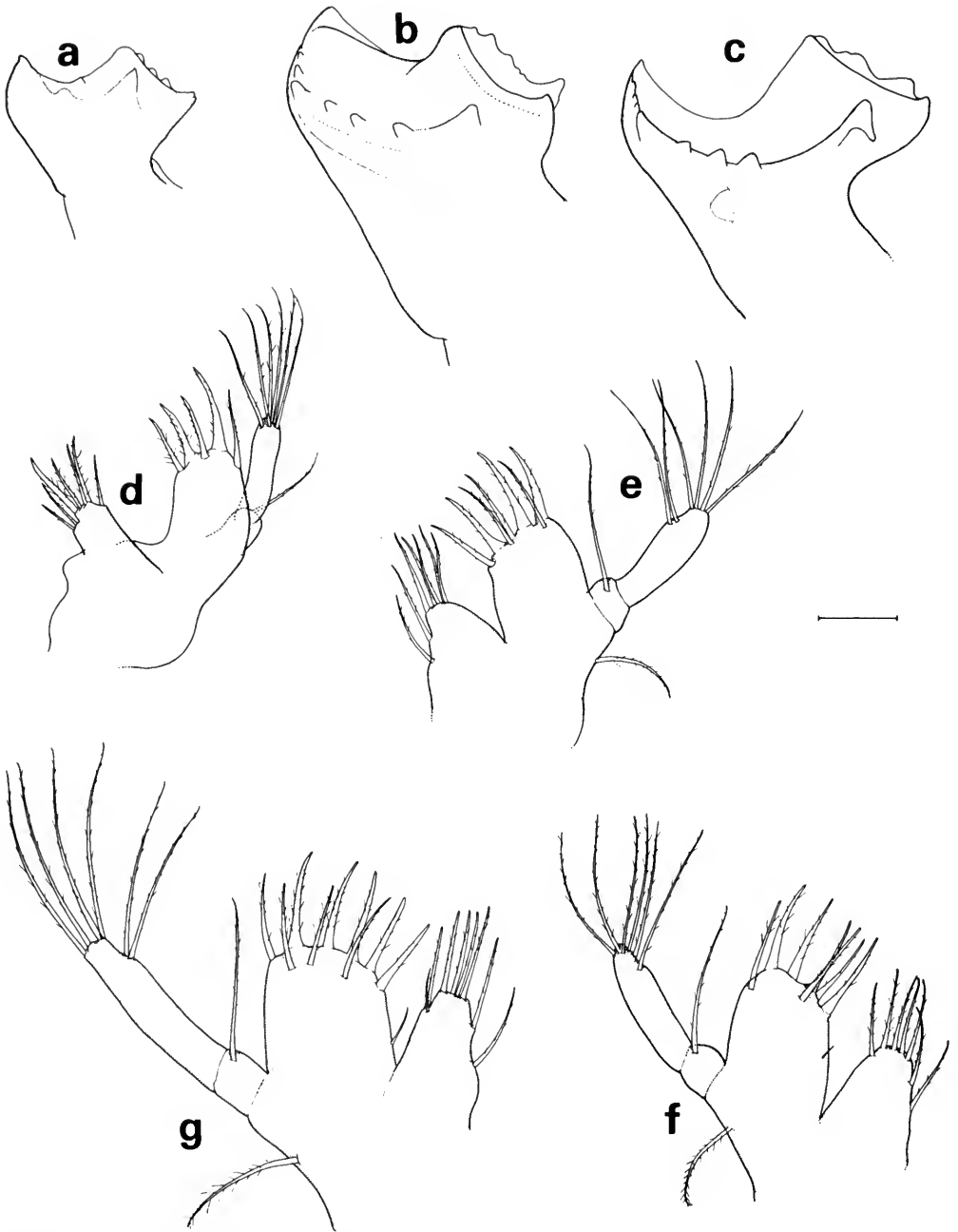
Fig. 3 *Cancer pagurus* L.: a–c right mandible of 1st, 4th, 5th zoeae; d–g maxillule of 1st–4th zoeae; scale = 0·05 mm.
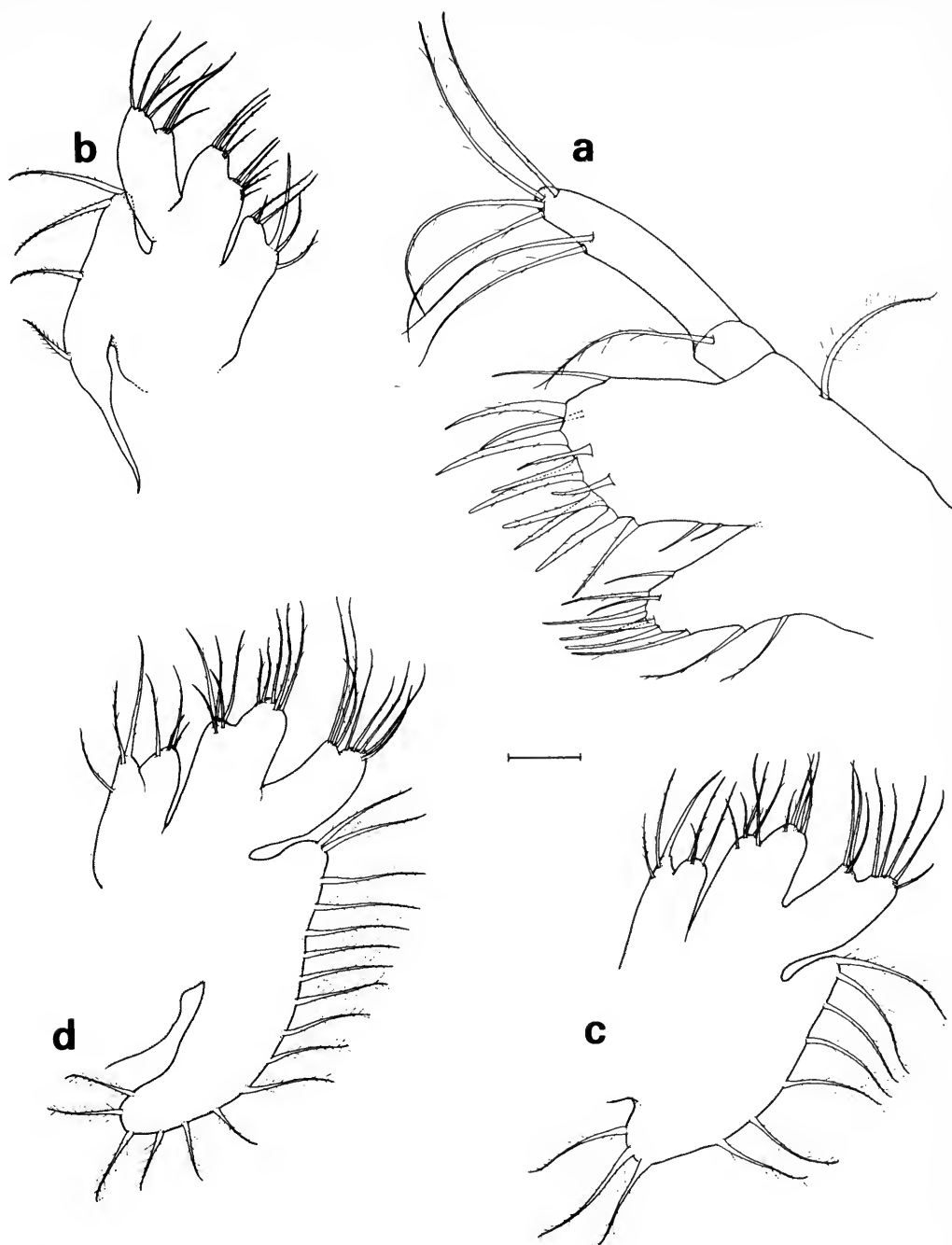
Fig. 4 *Cancer pagurus* L.: a maxillule 5th zoea; b–d maxilla 1st–3rd zoeae; scale = 0·05 mm.
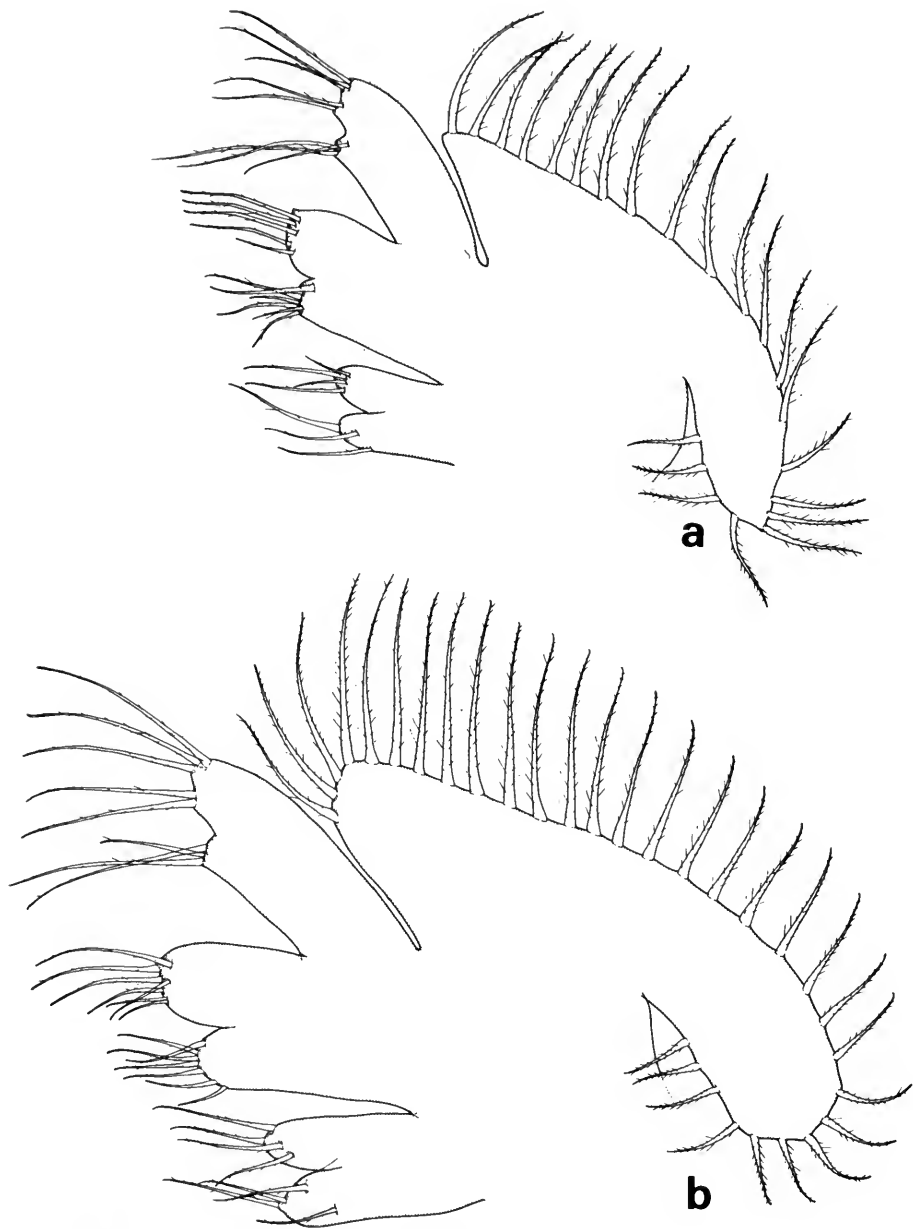
Fig. 5 *Cancer pagurus* L.: a–b maxilla 4th & 5th zoeae; scale as Fig. 4.
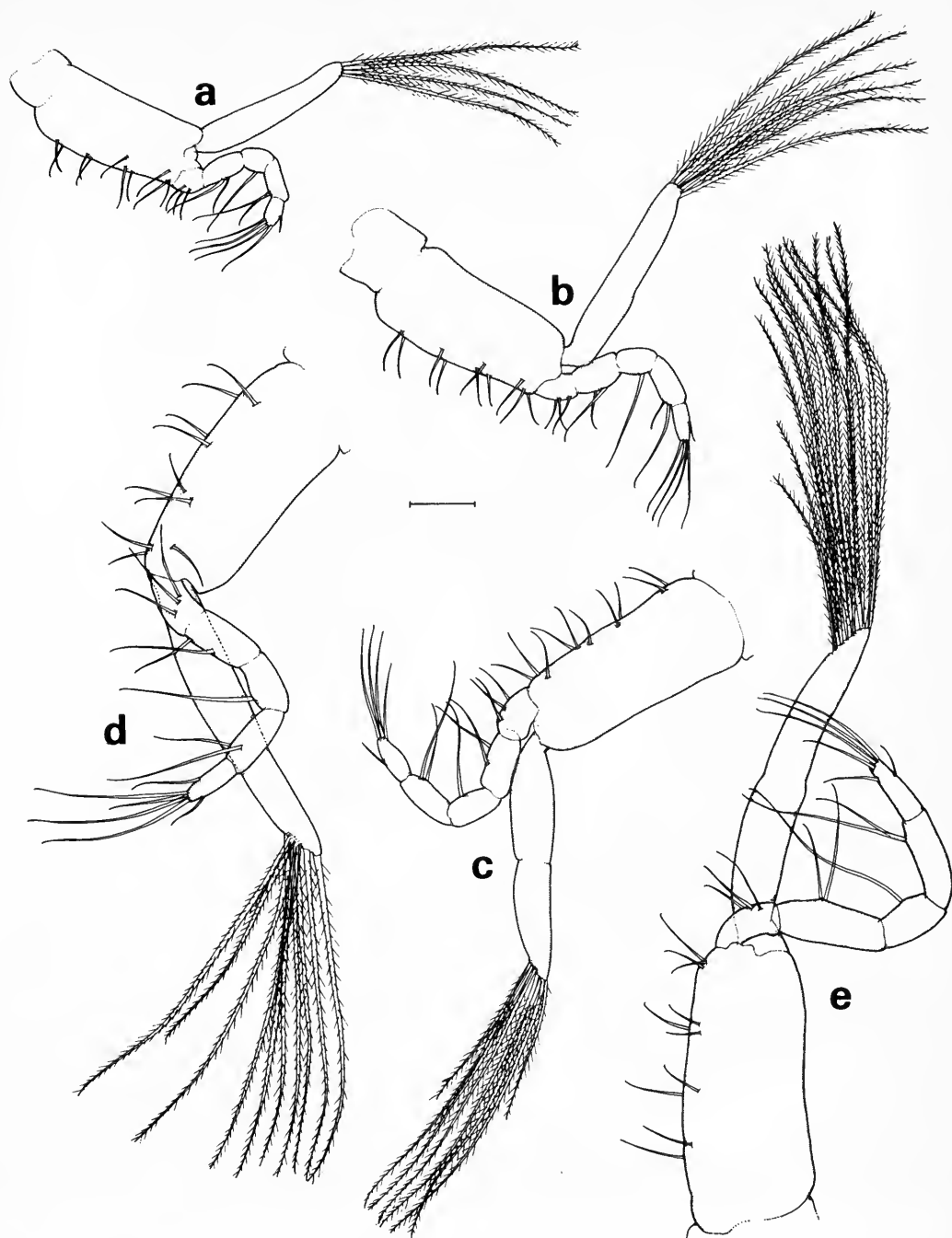
Fig. 6 *Cancer pagurus* L.: a–e first maxilliped 1st–5th zoeae; scale = 0·1 mm.
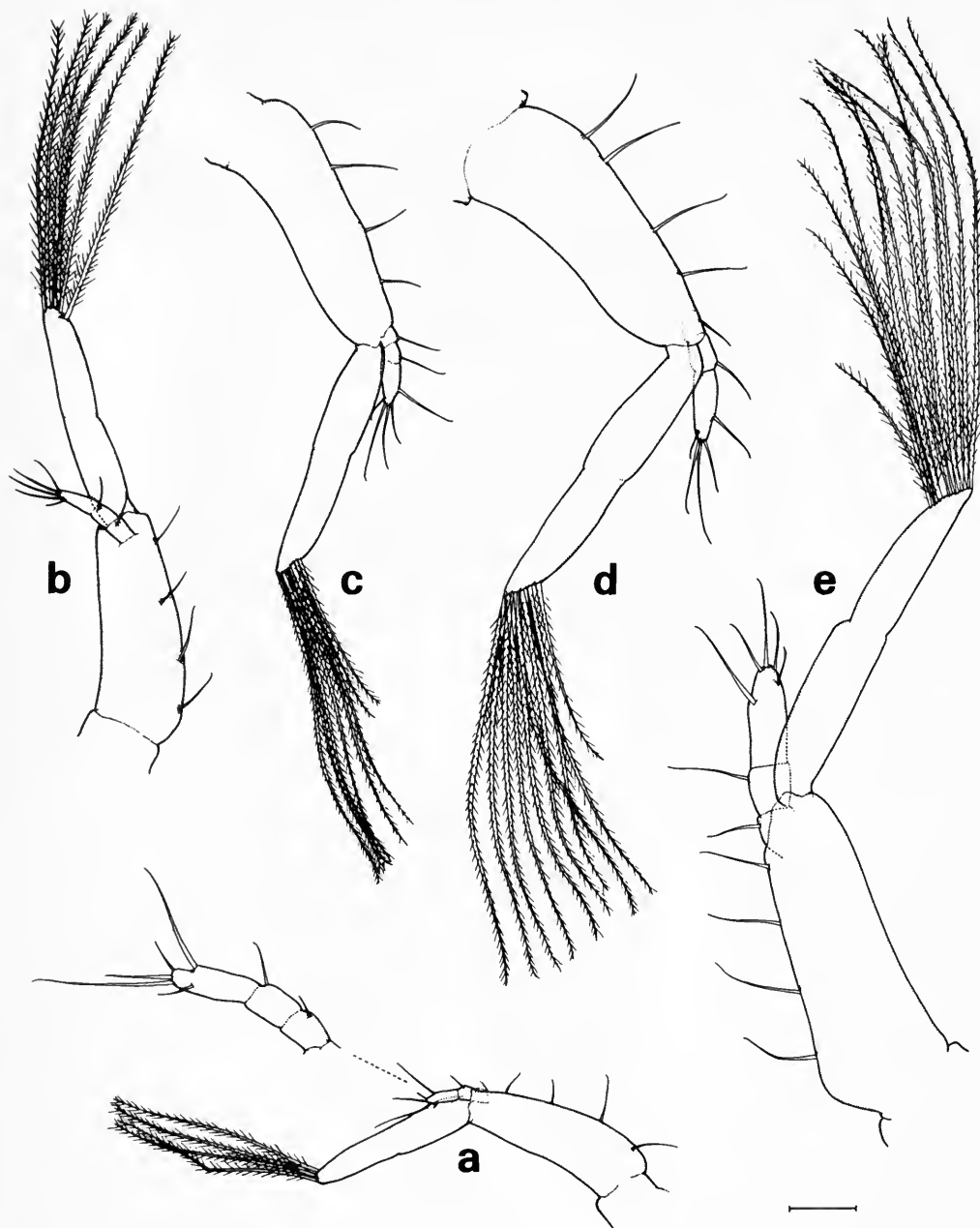
Fig. 7 *Cancer pagurus* L.: a–e second maxilliped 1st–5th zoeae; scale = 0·1 mm (inset to a endopod of another specimen at higher magnification).
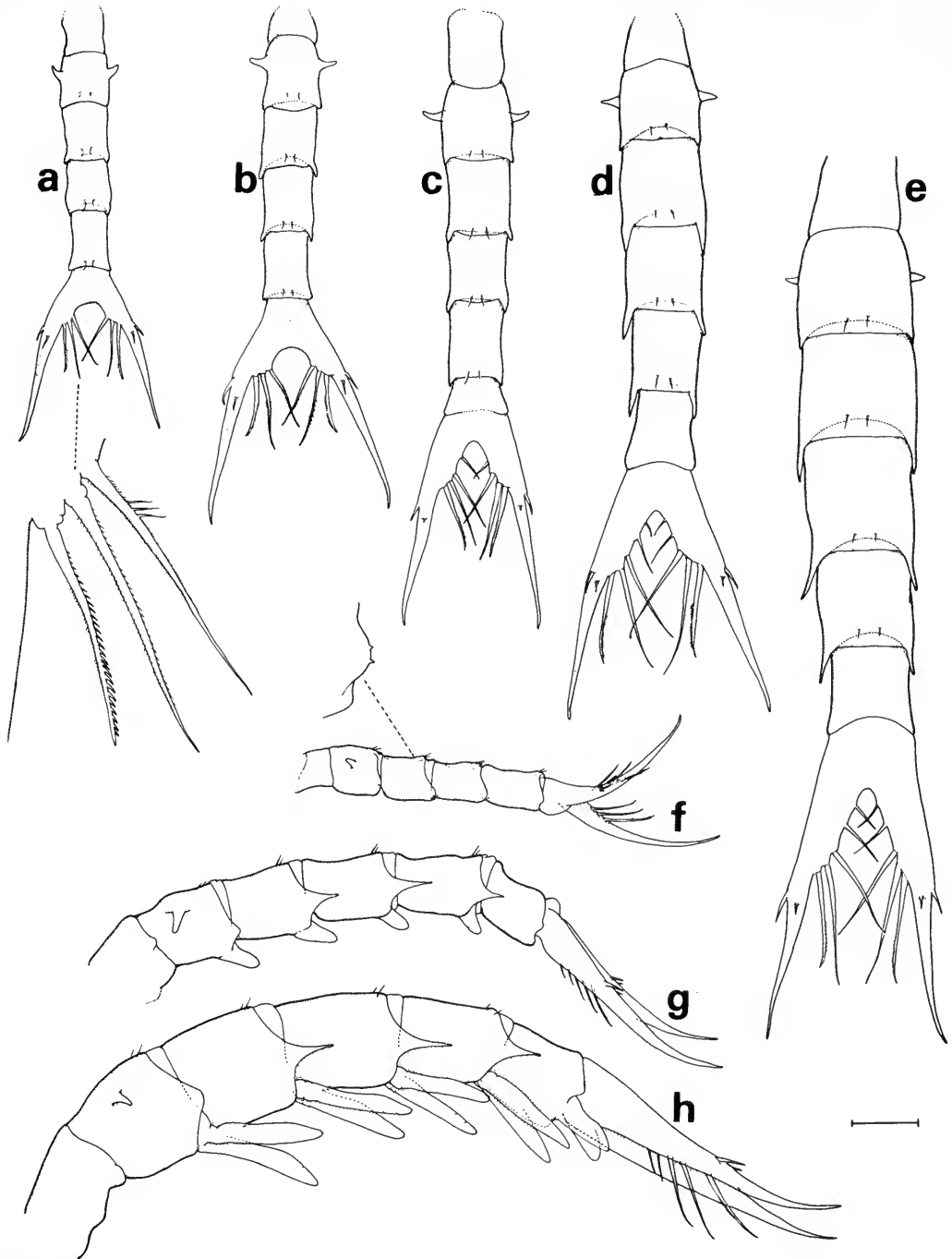
Fig. 8 *Cancer pagurus* L., abdomen and telson: a–e dorsal aspect of 1st–5th zoeae; f–h lateral aspect of 1st, 4th & 5th zoeae; scale = 0·2 mm (inset to f posterio-lateral margin of 3rd segment at higher magnification).
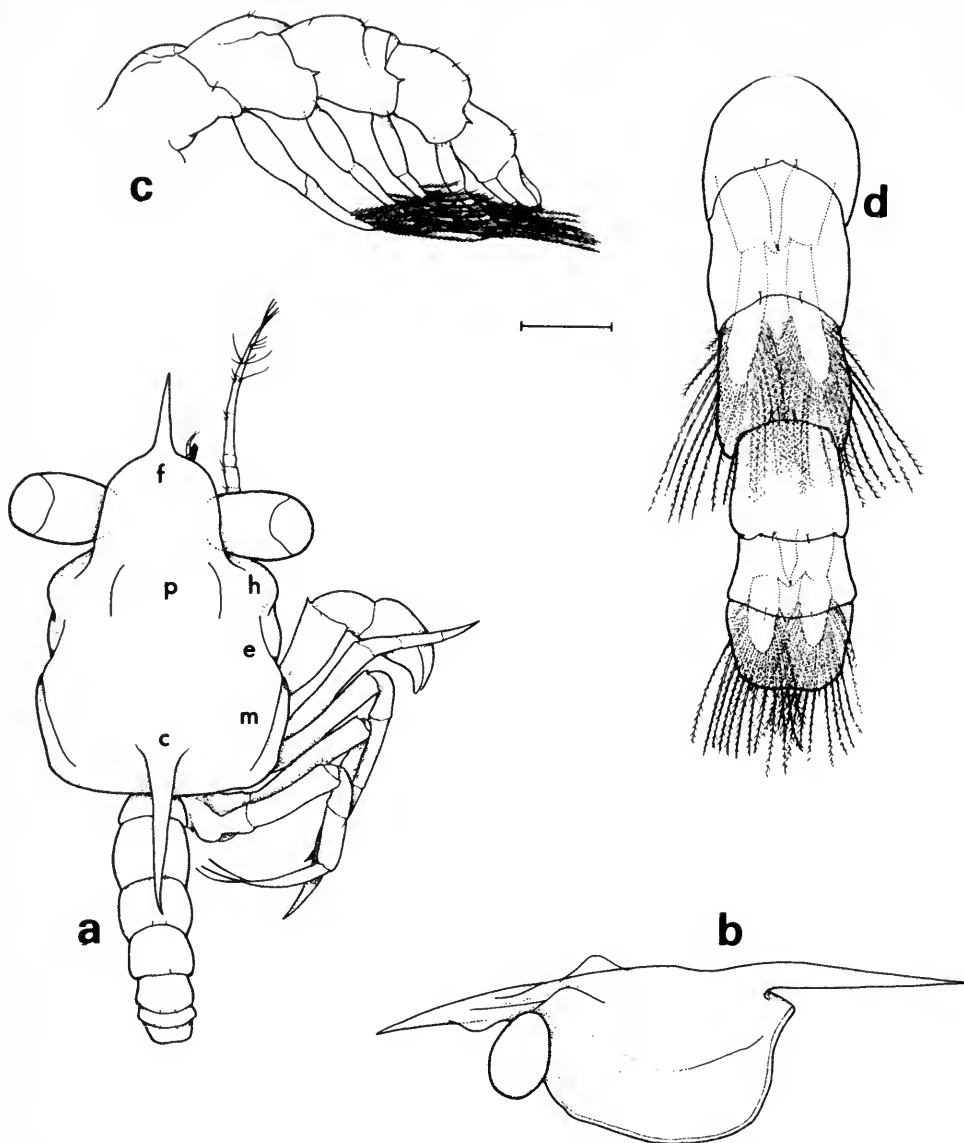
Fig. 9 *Cancer pagurus* L.: a dorsal aspect of megalopa; b lateral aspect of carapace; c–d abdominal segments 2–6 + telson from lateral & dorsal aspects (uropods omitted from d); c–d to scale 0·2 mm.
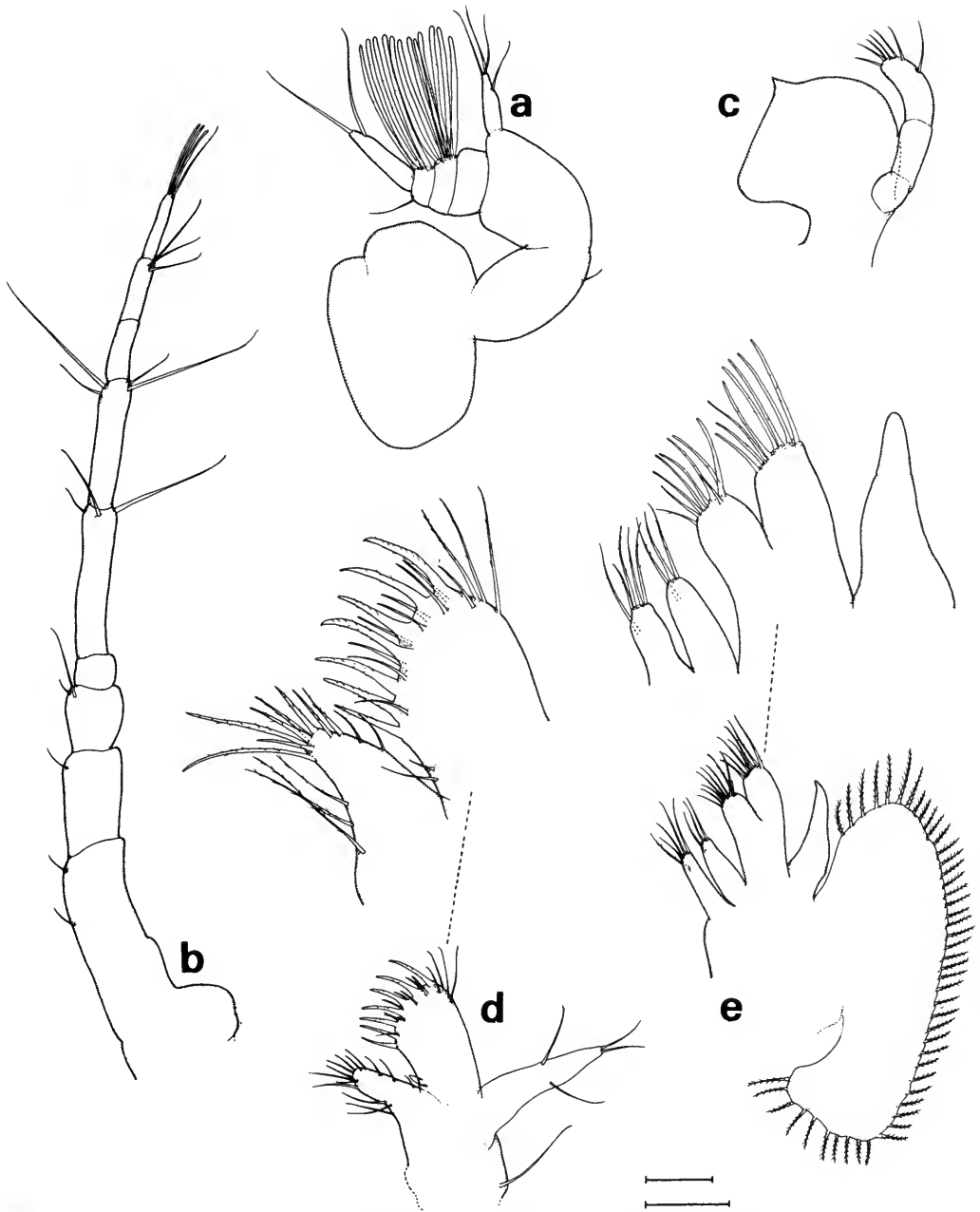
Fig. 10 *Cancer pagurus* L.: a antennule; b antenna; c mandible; d maxillule; e maxilla of megalopa; whole appendages to upper scale = 0·1 mm., inset to lower scale = 0·05 mm.
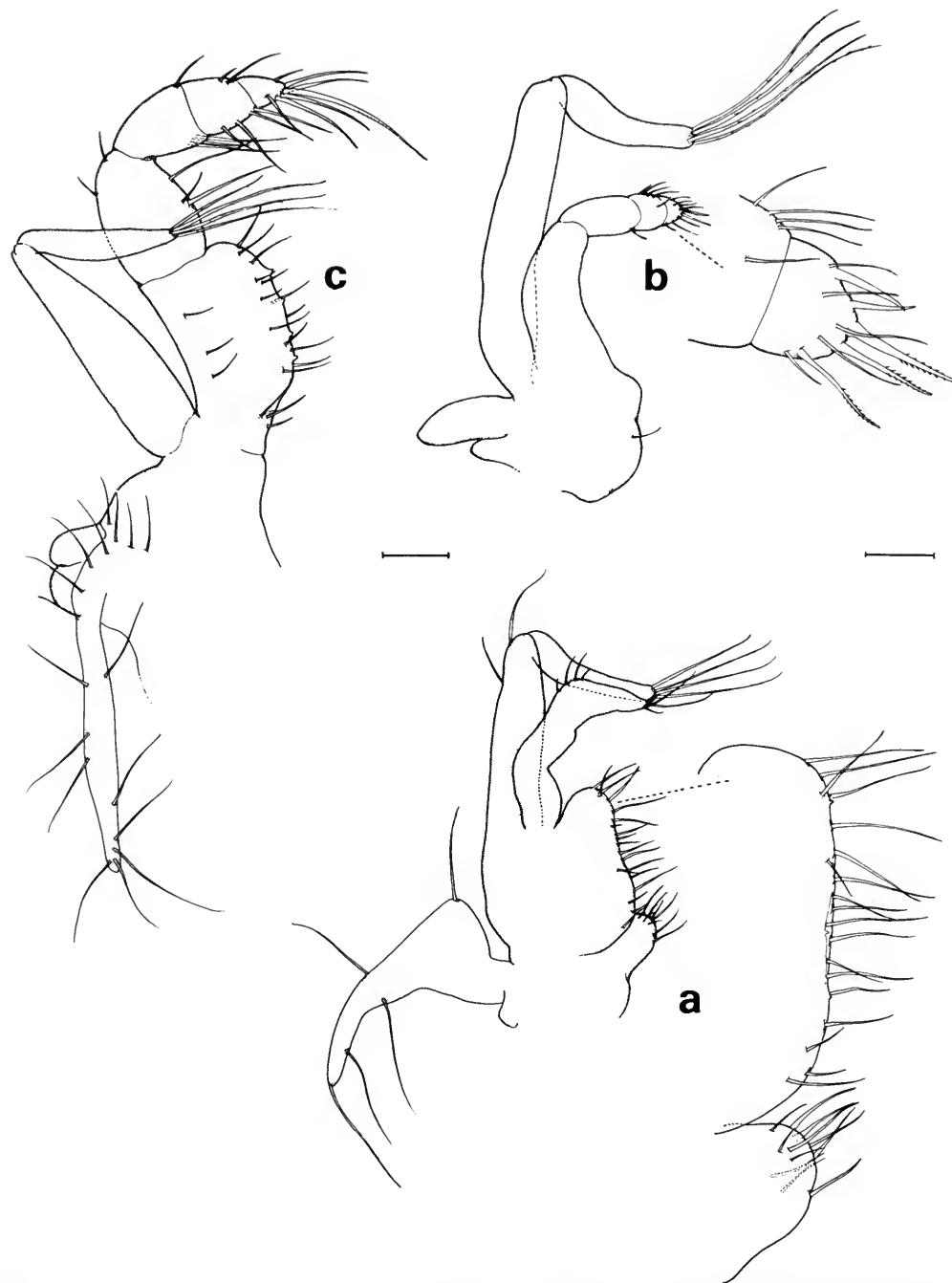
Fig. 11 *Cancer pagurus* L.: a–c 1st–3rd maxillipeds of megalopa; whole appendages to left scale = 0·1 mm., insets to right scale = 0·05 mm.
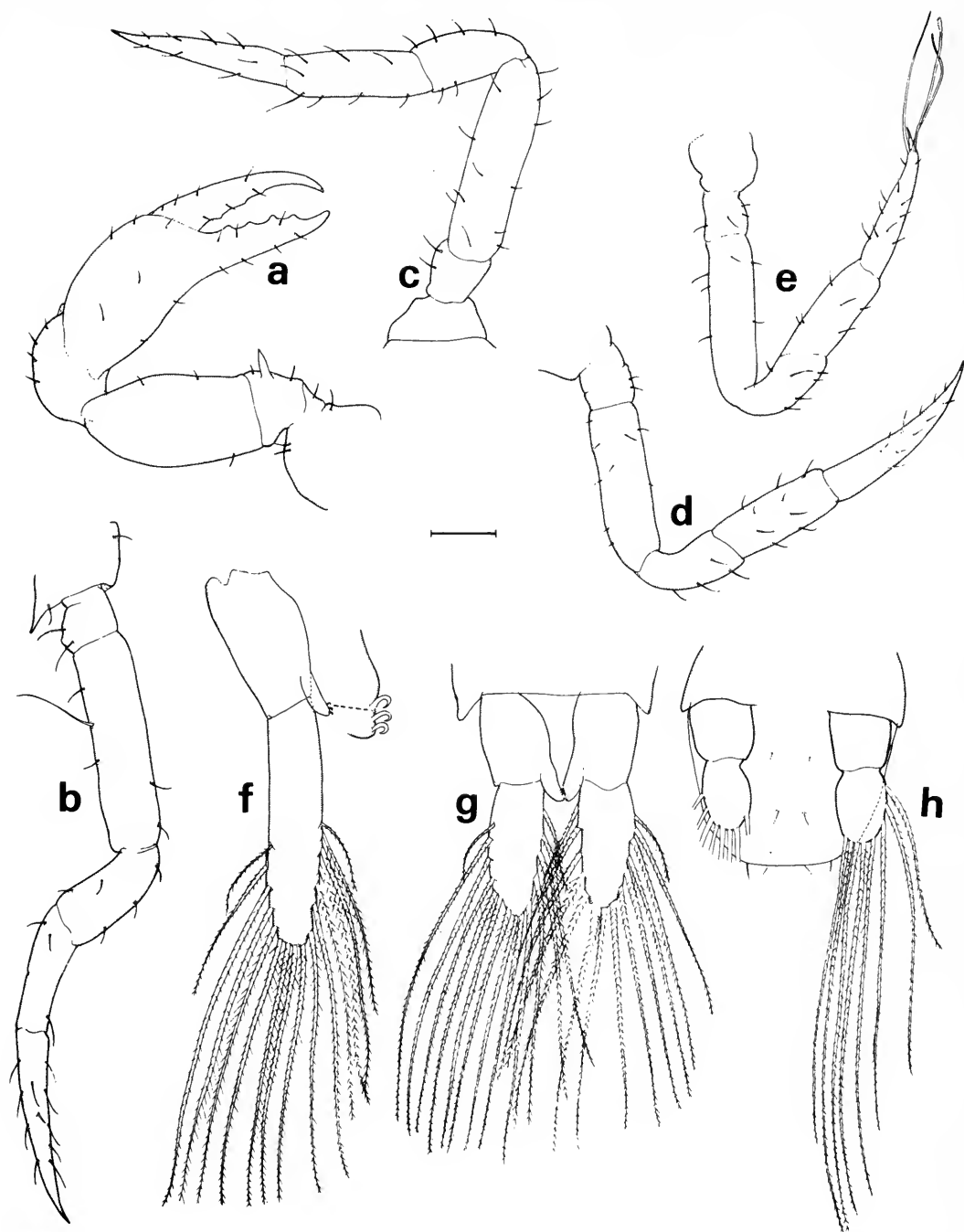
Fig. 12 *Cancer pagurus* L.: a–e 1st (= cheliped) to 5th pereiopod; f 1st pleopod; g 4th pair of pleopods; h 5th pair of pleopods and telson from ventral aspects all of megalopa; scales a–e = 0·2 mm., f–h = 0·1 mm.
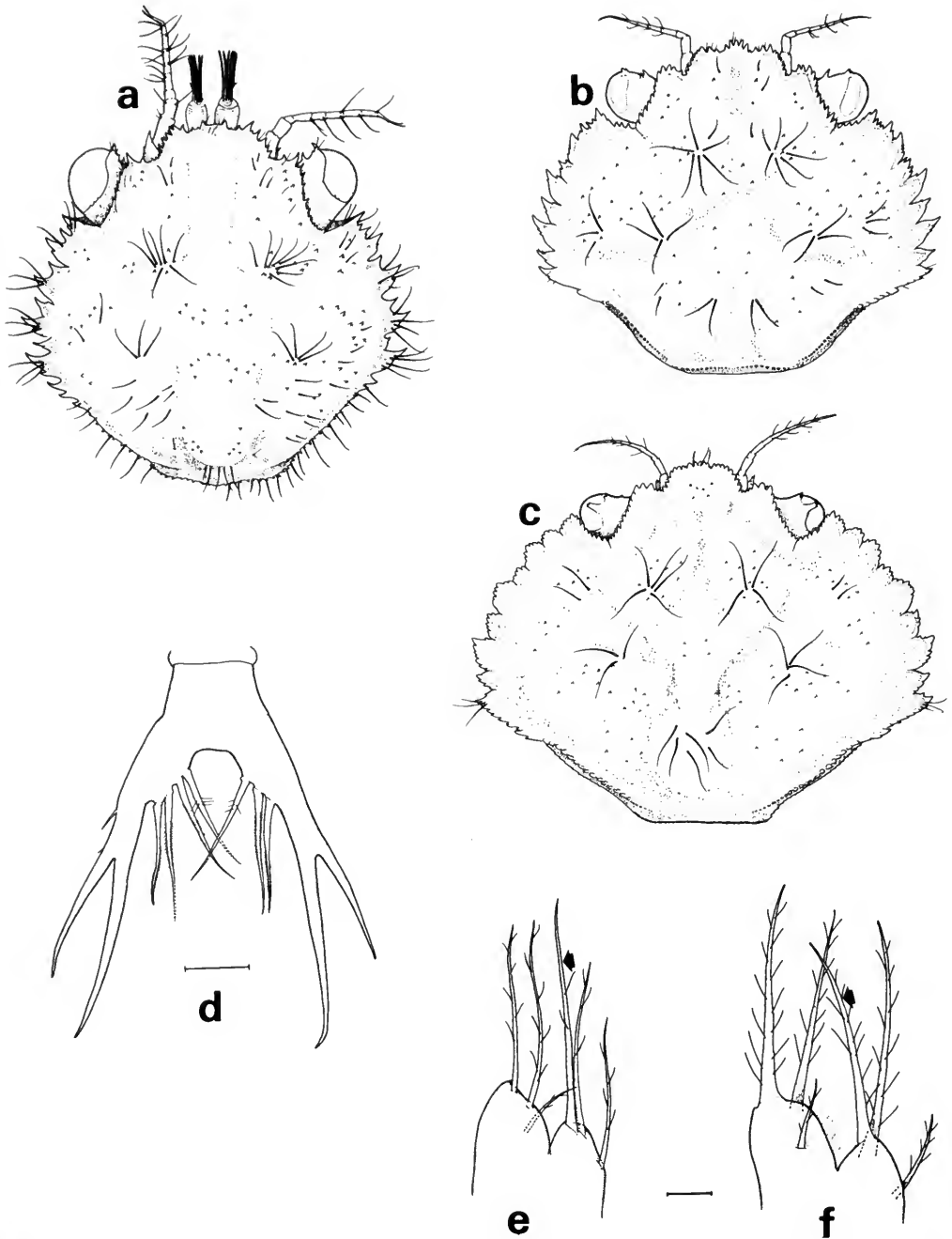
Fig. 13 *Cancer pagurus* L.: a–c carapaces of 1st–3rd crab stages measuring 2·5 mm., 3·0 mm & 4·0 mm C.L. respectively; d abnormal telson of first zoea from S. North Sea; scale = 0·1 mm. Coxal lobes of maxilla of, e *C. pagurus* L.; f *Liocarcinus puber* (Linnaeus); scale = 0·01 mm.

A taxonomic study of the larvae of four thalassinid species (Decapoda, Thalassinidea) from the Gulf of Mexico

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Introduction

Larvae of American mud-shrimps belonging to the superfamily Thalassinidae are poorly known. The complete larval stages of only three species have been described to date: *Upogebia pugettensis* (Dana) by Hart (1937), *Upogebia affinis* (Say) by Sandifer (1973) (family Upogebiidae), both described from plankton collected material, and *Naushonia crangonoides* Kingsley by Goy & Provenzano (1978), the first stage of which was described from plankton material and the remaining ones from laboratory reared specimens.

The recent material of decapod larvae from the Gulf of Mexico collected by the Virgilio Uribe Cruise (August 1972) contains numerous samples of thalassinid larvae from some stations (see Station List deposited in the Crustacea Section, British Museum (Natural History), London). Three species of *Upogebia*, one of which is probably *U. affinis* (Say), have been identified in this material and also a species belonging to the family Laomediidae and tentatively assigned to the genus *Axianassa*. The latter shows strong affinities to some larvae attributed by Menon (1933) to the subfamily Upogebiinae but is considered here as laomediid.

As two families of the Thalassinidea are considered in this Mexican plankton, it is convenient to discuss the representatives of each under separate headings:

A. Description of the larvae of three species of *Upogebia* Leach from the Gulf of Mexico with observations on larvae and adults of *Upogebia* in the collections of the British Museum (Natural History), London.
B. Description of the larvae of a species of the Laomediidae attributed to *Axianassa* from the Gulf of Mexico.
C. The relationship between larvae of the Laomediidae, those of the Upogebiidae and the adults of the Glypheidae.

Materials and methods

Larvae were sorted from plankton samples taken during the Virgilio Uribe Cruise during August 1972; they were preserved in 5% formalin. The size of the larvae given in the descriptions are the carapace length (c.l.) measured from the tip of the rostrum to the posterior border of the carapace in the mid-line, and the total length (t.l.) measured from the tip of the rostrum to the posterior margin of the telson. Drawings were made, using a *camera lucida,* from whole larvae or dissected appendages mounted in a drop of water.

A. Larval stages of three species of *Upogebia*

Three species of larval *Upogebia* can be recognized in the Mexican plankton material. No characters have been found that enabled the separation of the first larval stage which was

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Table 1 Comparison of the successive larval stages of *Upogebia* sp. A, *U. affinis* (Say) and *Upogebia* sp. B

	Upogebia sp. A	*U. affinis*	*Upogebia* sp. B
ZOEA I	the three species are indistinguishable		
ZOEA II			
Total length (mm)	2·35–2·45	2·30–2·55	2·72–2·80
Aesthetascs on antennule	3, all terminal	2, all terminal	4, all terminal
Setae on antennal scale	10–11	11–12	10
Mandible	without palp	without palp	without palp
Setae on basal endite of maxillule	4 + 3	4 + 3	4 + 3
Setae on exopod of maxilla	6–7	7	6
Setae on endopod of 3rd maxilliped	1	2	1–2
ZOEA III			
Total length (mm)	2·56–2·90	2·80–3·06	3·29–3·40
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	3, 1 subterminal
Setae on antennal scale	11–12	11–12	13
Mandible	without palp	without palp	without palp
Setae on basal endite of maxillule	4 + 3	4 + 3	4 + 3
Setae on exopod of maxilla	9–10	11–12	10
Setae on endopod of 3rd maxilliped	1	2	1–2
Setae on exopod of uropods	10–11	11–12	11–12
ZOEA IV			
Total length (mm)	2·85–3·00	3·00–3·57	3·80–4·00
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	4, 2 subterminal
Setae on antennal scale	12–13	13–14	14–15
Mandible	without palp	with palp	without palp
Setae on basal endite of maxillule	6 + 3	6 + 4 + 1	6 + 3
Setae on exopod of maxilla	10–11	13–14	12–13
Setae on endopod of 3rd maxilliped	1	0	1
Setae on uropods (exopod & endopod)	12–13, 9–10	13–15, 10–11	13–14, 10–11
ZOEA V			
Total length (mm)	3·12–3·63	3·90–4·00	4·82–5·44
Aesthetascs on antennule	3, 1 subterminal	3, 1 subterminal	4, 2 subterminal
Setae on antennal scale	12–13	13–14	14–16
Mandible	with palp	with palp	with palp
Setae on basal endite of maxillule	6 + 3	6 + 4 + 1	6 + 4 + 1
Setae on exopod of maxilla	14–15	13–14	12–14
Setae on endopod of 3rd maxilliped	0	0	0
Setae on uropods (exopod & endopod)	14–15, 10–12	13–15, 10–11	15–18, 14–16

abundant in all stations where the larvae were collected. The presence of the three species is therefore not recorded separately in the Station List.

From the second stage onwards each larval species can be distinguished by the combined characters listed in Table 1. The second species agrees with the larval description of *U. affinis* (Say) given by Sandifer (1973) and this material has been assigned to that species.

Description of the larval stages

The larvae of *Upogebia* sp. A are described in detail. Differences between the three species are observed in the size, the number and position of the antennular aesthetascs, the number of setae on the antennal scale, the presence or absence of a palp bud on the mandible, the number and arrangement of setae on the basal endite of the maxillule, the number of setae on the exopod of the maxilla and the endopod of the third maxilliped and also the number of setae on the uropods. The larvae of *U. affinis* and *Upogebia* sp. B are described with special consideration for these differential characters.

Upogebia sp. A

ZOEA I. From station CPOM 421 (18°54.5′N, 91°51′W) where apparently it is the only *Upogebia* sp. present.

    c.l. 0·70–0·75 mm

    t.l. 1·85–2·00 mm

Carapace (Fig. 1A) longer than broad with long rostral spine. Cervical groove present but very indistinct. Eyes partly fused to anterior margin of carapace.

Antennule (Fig. 1D) unsegmented with 3 aesthetascs and 2 setae distally and 1 subterminal plumose seta.

Antenna (Fig. 1C) exopod with 1 spine and 8–9 setae, endopod stout unsegmented with 3 apical setae, basis with 1 spine.

Mandible symmetrical with ventral part slightly expanded and without a palp.

Maxillule (Fig. 1F) endopod 3-segmented with 2, 2, 4 setae; basal endite with 5 setae placed into 2 rows, the lower with 2, the upper with 3 setae (setal formula of the basal endite can be written as 2 + 3); coxal endite with a single row of 6–7 setae.

Maxilla (Fig. 1E) scaphognathite with 5 marginal setae, endopod unsegmented with 6 setae, bilobed basal and coxal endites with 9–10 and 11–12 setae respectively.

First maxilliped (Fig. 1K) exopod 2-segmented with 4 apical setae, endopod 5-segmented with 3, 2, 1, 2, 5 setae, one seta on last segment being lateral; basis with 11, coxa with 2 setae respectively.

Second maxilliped (Fig. 1L) exopod 2-segmented with 4 apical setae, endopod 4-segmented with 2, 2, 2, 5 setae, 1 lateral seta on the last segment; basis with 2 setae.

Third maxilliped (Fig. 1M) exopod and endopod unsegmented and unarmed.

Pereiopods 1 and 2 (Figs 1G, H) exopods and endopods separated from basis, unsegmented and without setae.

Pereiopod 3 (Fig. 1I) elongated, biramous bud without setae.

Pereiopods 4 and 5 (Figs 1J4, J5) elongated, uniramous buds without setae.

Abdomen (Fig. 1A) 5-segmented, 5th segment with a pair of large lateral spines, 6th segment fused to telson.

Telson (Fig. 1B) roughly triangular with 7 + 7 spines, spine 2 reduced to a hair, anal spine present.

ZOEA II.   c.l. 0·85–0·90 mm

        t.l. 2·35–2·45 mm

Carapace (Fig. 2A) with eyes now free.

Antennule (Fig. 2D) now with an exopod demarcated from the peduncle with 3 aesthetascs and 3–4 setae and an endopod with 1 seta; peduncle with 2 large inner plumose setae and a few outer small ones.

Antenna (Fig. 2E) exopod with 1 spine and 10–11 setae, basis now with 2 spines.

Mandible (Fig. 2C) unchanged.

Maxillule (Fig. 2J) endopod unchanged, basal endite with 7 setae, setal formula 4 + 3; coxal endite with 7 setae.

Maxilla (Fig. 2I) scaphognathite with 6–7 setae, endopod unchanged, basal and coxal endites with 10 and 12 setae respectively.

First maxilliped (Fig. 2F) exopod now with 6 apical setae, endopod 5-segmented with 2, 3, 1, 2, 5 setae, second and last segments each with a lateral plumose seta.

Second maxilliped (Fig. 2G) exopod now with 6 apical setae, basis with 3 setae.

Third maxilliped (Fig. 2H) exopod now 2-segmented with 6 apical setae, endopod small with 1 plumose seta.

Pereiopod 1 (Fig. 2K) exopod now 2-segmented with 6 setae, endopod unsegmented and unarmed.

Pereiopods 2 and 3 (Figs 2L, M) exopods unsegmented, exopod of pereiopod 2 with 0–4 setae, exopod of pereiopod 3 without setae, endopods of both legs unsegmented and unarmed.

Pereiopods 4 and 5 (Figs 2N, O) exopods absent, endopods more elongated than in previous stage, unsegmented and unarmed.

Pleopods 2–5 (Fig. 2A) as small rounded buds.

Telson (Fig. 2B) now has an unarticulated median spine and a spine formula of 8 + 1 + 8, spine 2 reduced to a hair.

ZOEA III.   c.l. 1·02–1·10 mm
            t.l. 2·56–2·90 mm

Antennule (Fig. 3F) exopod still carrying 3 aesthetascs, one of which is now subterminal; endopod now separated from peduncle with 1 plumose seta, peduncle with 5 inner plumose setae.

Antenna (Fig. 3E) exopod with 1 spine and 11–12 setae, endopod now without setae, peduncle now 2-segmented.

Maxillule (Fig. 3C) endopod unchanged, basal endite with 4 + 3 setae, coxal endite with 8 setae.

Maxilla (Fig. 3D) scaphognathite with 9–10 setae.

First maxilliped (Fig. 3H) second segment of the endopod now with 4 setae one of which is lateral.

Second maxilliped (Fig. 3G) endopod 4-segmented with 2, 3, 3, 6 setae and with 1 lateral seta on the last segment.

Third maxilliped (Fig. 3I) endopod now larger still with 1 seta.

Pereiopods 1 and 2 (Figs 3J, K) exopods of both legs now 2-segmented with 6 apical setae, endopods large, unsegmented and unarmed.

Pereiopod 3 (Fig. 3L) both exopod and endopod unsegmented and unarmed.

Pereiopods 4 and 5, endopods now large.

Pleopods 2–5 (Fig. 3A) fairly large elongated buds on abdominal segments 2–5.

Abdomen (Fig. 3A) 6th abdominal segment now separated from telson with a pair of small dorsal spines on posterior border.

Telson (Fig. 3B) more elongated, setal formula unchanged.

Uropods (Fig. 3B) exopod and endopod not separated from basis, exopod with 10–11 setae, endopod unarmed.

ZOEA IV.   c.l. 1·05–1·15 mm
           t.l. 2·85–3·00 mm

Antennule (Fig. 4B) peduncle with 5–6 inner plumose setae, exopod with 3 aesthetascs one of which is subterminal.

Antenna (Fig. 4C) exopod with 12–13 setae.

Maxillule (Fig. 4D) basal endite with 9 setae placed in 2 rows, the lower with 6, the upper with 3 setae (setal formula of 6 + 3), coxal endite with 9–10 setae.

Maxilla, scaphognathite with 10–11 setae, endopod unchanged, basal and coxal endites now with 12–13 and 15–16 setae respectively.

First maxilliped (Fig. 3E) exopod with 6–8 setae, endopod unchanged.

Second maxilliped (Fig. 4F) exopod with 6–8 setae, endopod unchanged except for 1 lateral seta now present on second segment.

Third maxilliped (Fig. 4G) endopod unsegmented, large, still with 1 seta.

Pereiopods 1–3 (Figs 4H, I, J) exopods with 6 apical setae, endopods large, unsegmented.

Pereiopods 4 and 5 (Figs 4K, L) endopods large, unsegmented.

Pleopods 2–5 (Fig. 4A) larger than in previous stage.

Uropods (Fig. 4M) exopod and endopod now separated from basis, exopod with 12–13 setae, endopod with 9–10 setae.

Telson (Fig. 4M) approximately rectangular, spine formular unchanged but spine 2 is no longer hair-like, spine 4 largest and continuous with telson.

ZOEA V.　c.l. 1·19–1·32 mm
　　　　　t.l. 3·12–3·63 mm

Antennule (Fig. 5G) and *antenna* (Fig. 5F) unchanged.

Mandible (Fig. 5C) with a small rounded palp.

Maxillule (Fig. 5D) unchanged.

Maxilla (Fig. 5E) scaphognathite with 14–15 setae.

First and second maxillipeds (Figs 5I, J) unchanged.

Third maxilliped (Fig. 5H) exopod with 6–8 setae, endopod large, 5-segmented without setae.

Pereiopods 1–5 (Figs 5K–O) all endopods large and 5-segmented.

Pleopods 2–5 (Fig. 5P) uniramous, more elongated than in previous stage but still without a basis.

Uropods (Fig. 5B) exopod with 14–15 setae, endopod with 10–12 setae.

Telson (Fig. 5B) unchanged.

Upogebia affinis (Say)

ZOEA I. This stage cannot be distinguished from that of *Upogebia* spp. A or B.

ZOEA II.　c.l. 0·90–0·98 mm
　　　　　t.l. 2·30–2·55 mm

Antennule (Fig. 6D) exopod with 2 terminal aesthetascs and 4–5 small setae.

Antenna (Fig. 6E) exopod with 11–12 setae.

Mandible without a palp.

Maxillule (Fig. 6C) basal endite with 7 setae and a setal formula of 4 + 3.

Maxilla (Fig. 6F) scaphognathite with 7 marginal setae.

First and second maxillipeds (Figs 6G, H) do not differ from those of *Upogebia* sp. A.

Third maxilliped (Fig. 6I) endopod with 2 setae.

Periopod 2 (Fig. 6K) exopod usually unarmed.

ZOEA III.　c.l. 1·00–1·12 mm
　　　　　 t.l. 2·80–3·06 mm

Antennule (Fig. 7D) exopod with 3 aesthetascs one of which is subterminal, endopod demarcated from peduncle with 1 or 2 setae, peduncle with 3 distal and 5 inner plumose setae.

Antenna (Fig. 7E) exopod with 1 spine and 11–12 setae, endopod sometimes with 1 seta, peduncle with 2 spines.

Mandible without a palp.

Maxillule (Fig. 7F) basal endite with setal formula 4 + 3.

Maxilla scaphognathite with 11–12 marginal setae.

Third maxilliped (Fig. 7C) endopod with 2 setae.

Uropods (Fig. 7B) with 11–12 setae, endopod unarmed.

Zoea iv.   c.l. 1·15–1·22 mm
           t.l. 3·00–3·57 mm
   Antennule (Fig. 8C) exopod and endopod unchanged, peduncle with 6–7 inner plumose setae.
   Antenna exopod with 13–14 setae, endopod stout without setae.
   Mandible (Fig. 8B) now with a rounded palp.
   Maxillule (Fig. 8D) setae on basal endite now appear in 3 rows, the lowest with 6, the middle with 3–4 and the upper with 1 seta on the lateral side of the endite (setal formula 6 + 3–4 + 1), coxal endite with 10 setae.
   Maxilla scaphognathite with 13–14 marginal setae.
   Third maxilliped (Fig. 8E) endopod now unarmed.
   Uropods exopod with 13–15 setae, endopod with 10–11 setae.

Zoea v?   c.l. 1·36–1·40 mm
          t.l. 3·90–4·00 mm
Two specimens of this stage have been found. They differ from larvae of the previous stage by their larger size (Fig. 8G), their larger third maxilliped (Fig. 8H) and pereiopods (Figs 8I–M) the endopods of all of which are 5-segmented. It is not known whether they constitute a separate stage or are only a further developed stage IV. Sandifer (1973) reported 4 stages in the larvae of *U. affinis* of Virginia plankton while according to M. H. Roberts (see Sandifer, 1973) this species passes through 4 or 5 (usually 4) stages in laboratory rearing.

Remarks. The material examined agrees in most features with the larvae of *U. affinis* described by Sandifer (1973), except that the antennular exopod of Zoea II has 4–5 instead of 6 setae, the maxilla scaphognathite of Zoea II has 7 marginal setae instead of 6 and that of Zoea III has 11–12 setae instead of 9–10.

Upogebia sp. B

This species differs from the two previous ones by its larger size although stage I cannot be distinguished from that of *Upogebia* sp. A or *U. affinis*.

Zoea ii.   c.l. 0·95–1·10 mm
           t.l. 2·72–2·80 mm
   Antennule (Fig. 9C) exopod with 4 terminal aesthetascs.
   Antenna exopod with 10 marginal setae.
   Mandible without a palp.
   Maxillule endopod 3-segmented with 2, 2, 4 setae, basal endite with 4 + 3 setae, coxal endite with 7 setae.
   Maxilla exopod with 6 setae.
   Third maxilliped (Fig. 9D) endopod small with 1 or 2 setae.
   Pereiopod 1 (Fig. 9E) exopod with 4 setae, endopod fairly small, without setae.
   Pereiopod 2 (Fig. 9F) exopod with 0–4 setae.
   Pereiopod 3 (Fig. 9G) biramous bud, exopod unarmed.

Zoea iii.   c.l. 1·19–1·22 mm
            t.l. 3·29–3·40 mm
   Antennule (Fig. 9I) exopod with 3 aesthetascs one of which is subterminal, endopod with 2 setae.
   Antenna exopod with 13 marginal setae.
   Maxillule basal endite with 4 + 3 setae, coxal endite with 8 setae.
   Maxilla scaphognathite with 10 setae.
   Third maxilliped (Fig. 9J) endopod with 1–2 setae.
   Uropods (Fig. 9K) basis not yet differentiated, exopod with 11–12 setae, endopod unarmed.

ZOEA IV.   c.l. 1·36–1·40 mm
                t.l. 3·40–4·00 mm

Antennule (Fig. 10D) exopod now with 4 stout aesthetascs 2 of which are subterminal.
Antenna exopod with 14–15 setae.
Mandible without a palp.
Maxillule (Fig. 10C) endopod unchanged, basal endite with 6 + 3 setae, coxal endite with 9 setae.
Maxilla scaphognathite with 12–13 setae.
Third maxilliped (Fig. 10E) endopod with 1 seta.
Uropods (Fig. 10B) basis now differentiated, exopod with 13–14 setae, endopod with 10–11 setae.

ZOEA V.   c.l. 1·66–1·76 mm
               t.l. 4·82–5·44 mm

Antennule (Fig. 10H) exopod still with 4 aesthetascs 2 of which are subterminal.
Antenna exopod with 14–16 setae.
Mandible (Fig. 10G) with a palp.
Maxillule (Fig. 10I) basal endite with 6 + 4 + 1 setae, coxal endite with 10–11 setae.
Maxilla scaphognathite with 12–14 setae.
Third maxilliped (Fig. 10J) endopod 5-segmented, without setae.
Pereiopods 1, 2, 3 (Fig. 10K) exopods with 7, 7 and 6 setae respectively, endopods 5-segmented.
Pereiopods 4, 5 endopods 5-segmented.
Uropods exopod with 15–18 setae, endopod with 14–16 setae.

Discussion

The three Mexican larval species studied closely resemble one another and show many similarities with other *Upogebia* larvae previously described. They nevertheless differ from all but one species by having a pair of large lateral spines on the 5th abdominal segments and a pair of small dorsal spines on the posterior border of the 6th. These spines constitute the main features of interest. They were recorded with certainty for the first time by Sandifer (1973) in *U. affinis* from Virginia although one larval species with lateral spines on the 5th abdominal segment was tentatively assigned to *Upogebia* by Dakin & Colefax (1940). The presence of abdominal spines can be considered as an important distinguishing character separating the 3 present American *Upogebia* species, and possibly also the Australian one described by Dakin & Colefax, (1940), from all the remainder. In order to establish whether these spines are present on other *Upogebia* larvae from other regions of the world, larval material in the collections of the BMNH were examined. This included specimens from widely separated geographical regions as the Great Barrier Reef (BM 1951.2.17.2111–2140), the Red Sea (BM 1951.2.17.2103–2110), Nosy Bé (Madagascar) and the Gulf of Guinea. Lateral spines were not found on the 5th abdominal segment of any of these specimens but larvae from the Great Barrier Reef, the Red Sea and Nosy Bé have a small median spine on the posterior border of the 6th abdominal segment from stage III onwards (see Figs 11A, B). In the material from the Gulf of Guinea which includes two or more species, the median spine is present in some larvae and absent in others. Therefore, with respect to the presence of abdominal spines, *Upogebia* larvae do not constitute a zoogeographical homogenous group whilst the absence of lateral spines from the abdomen can no longer be taken as a character holding good for all of them.

Gurney (1938) suggested that the Laomediidae and Upogebiidae are related. As discussed later in this work, one group of laomediid larvae assigned to *Axianassa* sp. and its relatives, have features that link these two families, whilst the presence of a pair of lateral spines on the 5th abdominal segment place them near the Mexican *Upogebia* material described above.

To discover if the grouping of the larvae suggested above also holds good for the adults, and to evaluate the relationship of the genus *Upogebia* with the Laomediidae, adults of the following species of *Upogebia* were examined in the collections of the BMNH.

Species	Origin of the material
U. acutispina de Saint Laurent & Ngoc-Ho	Holothuria Bank, Australia
U. affinis (Say)	S. Carolina, Georgia, USA
U. africana Ortmann	South Africa
U. brasiliensis Holthuis	British Guiana
U. carinicauda (Stimpson)	Thursday Island
	Gulf of Siam
	Madagascar
U. danai (Miers)	Cape Campbell, N. Zealand
U. darwini (Miers)	Phuket, Thailand
	Singapore
	Port Darwin
U. deltaura (Leach)	Plymouth, Britain
	Galway, Ireland
U. giralia Poore & Griffin	Australia
U. hirtifrons (White)	South Seas (Antarctic)
U. issaeffi (Balss)	Tsur Island, Japan
U. lincolni Ngoc-Ho	Java, Indonesia
U. littoralis (Risso)	Napoli, Italy
	Malta
U. major de Haan	Japan
U. miyakei Sakai	Japan
U. omissa Correa	Brazil
U. pugettensis (Dana)	California, USA
U. savignyi (Strahl)	Red Sea
U. simsoni (Thomson)	Australia
U. spinigera (Smith)	Ecuador
	Peru
U. stellata (Montagu)	Plymouth, Britain
	Galway, Ireland
Upogebia sp.	North Kenya
U. talismani Bouvier	Ivory Coast, Africa

The following species were also considered as their descriptions and illustrations (Bozic & de Saint Laurent, 1972; Le Loeuff & Intes, 1974; de Saint Laurent & Ngoc-Ho, 1979) are adequate for comparison (except for the branchial structure of all but one of them, which has been completed by examination of the material deposited at the Museum national d'Histoire naturelle, Paris):

U. aristata Le Loeuff & Intes	Ivory Coast, Africa
U. contigua Bozic & de St Laurent	Gulf of Guinea
U. crosnieri Le Loeuff & Intes	Ivory Coast, Africa
U. furcata (Aurivillius)	Ivory Coast, Africa
U. nitida (A. Milne-Edw.)	Ivory Coast, Africa
U. poensis de St Laurent & Ngoc-Ho	Fernando Po, Gulf of Guinea

Variations in the adult material of *Upogebia* examined concern the presence or absence of an epipod on the maxillipeds, of a large dorsal tooth on the mandible and also the form of the arthrobranchs. Taking *U. issaeffi* as an example, all its 3 maxillipeds (Figs 11D, E, F) have each an exopod, an epipod on the coxa and the 2nd maxilliped to the 4th pereiopod has a pair of arthrobranchs. Its branchial formula can be written as follows:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Pleurobranchs	–	–	–	–	–	–	–	–
Arthrobranchs	–	2	2	2	2	2	2	–
Podobranchs	–	–	–	–	–	–	–	–
Epipods	1	1	1	–	–	–	–	–
Exopods	1	1	1	–	–	–	–	–

In *U. issaeffi* as well as in all other *Upogebia* species, an epipod is always present on the 2nd maxilliped.

In *U. issaeffi*, the arthrobranchs consist of a fairly large and flattened structure on either side of the rachis (Fig. 12A) and are referrred to as arthrobranchs type A. The mandible (Fig. 11C) is devoid of a dorsal tooth. In some other species, such as *U. savignyi,* epipods are absent from both the first and the third maxillipeds and arthrobranchs are of type B, with a

Table 2 Various species of *Upogebia* compared according to their epipods, arthrobranchs and other characteristics

Species	Characteristics				
	Epipods on Mxp 1	Mxp 3	Type of arthrobranchs	Dorsal tooth on mandible	Subgeneric division, after de Man
1. *U. affinis*	+	+	A	–	(U)
U. brasiliensis	+	+	A	–	(U)
U. hirtifrons	+	+	A	–	(U)
U. issaeffi	+	+	A	–	(U)
U. major	+	+	A	–	(U)
U. omissa	+	+	A	–	(U)
U. pugettensis	+	+	A	–	(U)
U. spinigera	+	+	A	–	(U)
2. *U. danai*	–	–	A	–	(U)
U. darwini	–	–	A	–	(C)
U. hexaceras	–	–	B	–	(C)
U. savignyi	–	–	B	–	(C)
U. simsoni	–	–	A	–	(U)
Upogebia sp.	–	–	B	–	(C)
3. *U. carinicauda*	+	–	C	–	(U)
U. giralia	+	–	C	–	(U)
4. *U. acutispina*	–	+	B	–	(U)
U. africana	–	+	C	+	(U)
U. aristata	–	+	C	+	(U)
U. contigua	–	+	B	–	(U)
U. crosnieri	–	+	C	+	(C)
U. deltaura	–	+	C	+	(C)
U. furcata	–	+	C	+	(C)
U. lincolni	–	+	C	–	(U)
U. littoralis	–	+	C	+	(U)
U. miyakei	–	+	C	–	(U)
U. nitida	–	+	C	+	(C)
U. poensis	–	+	C	+	(U)
U. stellata	–	+	C	+	(U)
U. talismani	–	+	B	–	(U)

slightly flattened tubular structure on either side of the rachis (Fig. 12B). The mandible has no dorsal tooth. In *U. deltaura,* epipods are present on the second and third maxillipeds but not on the first (Fig. 12G); arthrobranchs are similar to those of *U. stellata* (Fig. 12C), of type C, with 2 small tubular structures on either side of the rachis. The mandible is provided with a large dorsal tooth (Fig. 12F). *U. carinicauda,* on the other hand, has epipods on the first and the second maxillipeds, arthrobranchs of type C and no tooth on the mandible.

Upogebia species considered in this work are separated into groups below according to their epipods, arthrobranchs and mandible characteristics:

(a) Presence (+) or absence (−) of epipods on the first and third maxilliped. A minute epipod on the first maxilliped (Fig. 12E) is disregarded.

(b) Type of arthrobranchs, A, B or C.

(c) Presence (+) or absence (−) of a dorsal tooth on the mandible. When present, this tooth may be small (Fig. 12D) or large (Fig. 12F).

For comparison, the subdivision of *Upogebia* by de Man (1928) into 2 subgenera, *Upogebia (Upogebia)* Leach and *Upogebia (Calliadne)* Strahl is here included. To subgenus *Upogebia* de Man assigned the species with a spine on the antero-lateral margin of the carapace and in which the fixed finger of the cheliped is shorter than the dactylus, while he placed species in which the antero-lateral carapace is absent and the fixed finger is as long as the dactylus into the sub-genus *Calliadne.* Species are here referred to as:

(d) ·Belonging to subgenus *Upogebia* ((U)) or subgenus *Calliadne* ((C)), after de Man.

The foregoing study (Table 2) reveals that:

(a) Although the species in groups 1 & 3 can be assigned to de Man's subgenus *Upogebia,* those belonging to groups 2 & 4 are divided between his subgenus *Upogebia* and *Calliadne* and are seen to be associated indifferently with any type of epipod, of arthrobranch or mandible. It would be necessary to examine more material before refuting or substantiating completely the subdivision of the genus *Upogebia* as suggested by de Man, nevertheless, the limited amount of material examined shows that these divisions should not be upheld at present.

(b) The American *Upogebia* belong to the first group that contains species with an epipod on both the first and third maxillipeds. As a reduction of the gill formula is generally considered as an advanced character, *Upogebia* species of the first group would be, in this respect, more primitive than the remainder. They are also more similar to the Laomediidae in all known species of which, epipods are present on all maxillipeds. According to Le Loeuff & Intes (1974), the branchial formula is very homogenous in laomediids, and in *Jaxea novae-zealandiae* Wear & Yaldwyn, it is as follows:

	Maxillipeds			Pereiopods				
	1	2	3	1	2	3	4	5
Arthrobranchs	2	2	2	2	2	2	2	−
Podobranchs	−	1	1	1	1	1	1	−
Epipods	1	1	1	1	1	1	1	−
Exopods	1	1	1	−	−	−	−	−

On the other hand, the flattened arthrobranch of type A found in species of the first group is similar to that of the Laomediidae (see Wear & Yaldwyn, 1966; Le Loeuff & Intes, 1974) and could be considered as the most primitive of the 3 types. The species of this group possess characters of the subgenus *Upogebia,* and some, such as *U. affinis* and its relatives, produce larvae with a pair of lateral spines on the fifth abdominal segment; these are probably also primitive features. Nevertheless, there is variation in the larval morphology within the same group as abdominal spines are absent from the larvae of *U. pugettensis* (Hart, 1937) and *U. major* (Kurata, 1965).

(*c*) In the second group of species arthrobranchs of type A and B are found. Type B, with a single slightly flattened structure on either side of the rachis, is somewhat similar to type A and suggests the next stage in the evolution of arthrobranchs in *Upogebia* along with the disappearance of the epipods from both the first and the third maxillipeds.

(*d*) In the third and fourth groups of species arthrobranchs of type C are generally found and they probably represent the most evolved type in *Upogebia*. Epipods have now reappeared either on the first or the third maxilliped and a group of African and Mediterranean species, i.e. *U. crosnieri, U. deltaura,* appear to have developed a dorsal tooth on the mandible at this stage of evolution.

(*e*) The above suggestions of evolutionary trends in the Upogebiidae are speculative. They agree with the recent work by de Saint Laurent & Le Loeuff (1979) in the following points: 1. Primitive forms of the family would have a subcheliform pereiopod 1;   2. The presence of an antero-lateral carapace spine is probably another primitive character;   3. There would be a tendancy during evolution towards the disappearance of epipods on the first maxilliped.

However the suggestions presented here disagree with the above mentioned authors who regard arthrobranchs of type A ('*lamelles branchiales larges et entières*') as the most evolved form and consider that the American group of *Upogebia* as advanced rather than primitive. Besides having arthrobranchs of type A, American species examined in this work are provided with certain characters also considered by de Saint Laurent & Le Loeuff as primitive. These are the presence of an epipod on the first maxilliped, a subcheliform pereiopod 1 and an antero-lateral carapace spine.

(*f*) De Saint Laurent & Le Loeuff (1979) also suggested the grouping of known species of *Upogebia* and discussed the relationship of those of the Atlantic and East Pacific. The conclusions based on the limited amount of material examined here agree in general with this.

B. Larvae of a species of Laomediide attributed to *Axianassa*

Description of the larval stages

ZOEA I.   c.l. 0·85–0·90 mm
          t.l. 2·00–2·10 mm

Carapace (Figs 13A, B) longer than broad with long rostral spine. Cervical groove present but indistinct. Eyes fused to anterior margin of carapace.

Antennule (Fig. 13C) unsegmented with 3 aesthetascs and 2 setae distally and a subterminal plumose seta.

Antenna (Fig. 13D) exopod with 1 spine and 10 setae, endopod stout with 3 apical setae, peduncle with 1 spine.

Mandibles (Fig. 13E) asymmetrical with the left one sickle-shaped. Left lobe of paragnath (Fig. 11L) also sickle-shaped.

Maxillule (Fig. 13F) endopod unsegmented with 3 apical setae, basal and coxal endites each with 4 setae.

Maxilla (Fig. 13G) scaphognathite with 5 setae, endopod small, unsegmented with 2 setae, bilobed basal and coxal endites carrying 8 and 5 setae respectively.

First maxilliped (Fig. 13H) exopod 2-segmented with 4 apical setae, endopod 4-segmented with 1, 1, 2, 5 setae one of which is lateral on last segment; the basis has 4 setae.

Second maxilliped (Fig. 13I) exopod 2-segmented with 4 apical setae, endopod 4-segmented, penultimate and last segment with 2 and 4 setae respectively, coxa and basis unarmed.

Third maxilliped (Fig. 13J) exopod 2-segmented without setae, endopod absent.

First and second pereiopods as small rounded buds.

Abdomen (Figs 13A, B) 5-segmented, 5th segment bearing a pair of large lateral spines, 6th segment fused with telson.

Telson (Fig. 13K) spatuliform, with a median hollow and 7 + 7 spines, spine 2 reduced to a hair.

ZOEA II.   c.l. 0·95–1·00 mm
           t.l. 2·1–2·2 mm

Carapace (Fig. 14A) with eyes now free from the carapace.
Antennule (Fig. 14D) unchanged.
Antenna (Fig. 14E) exopod with 1 spine and 13 setae, basis with 2 spines.
Maxillule (Fig. 14G) endopod and coxal endite unchanged, basal endite now with 5 setae.
Maxilla (Fig. 14F) scaphognathite with 7 setae.
First maxilliped (Fig. 14I) exopod with 6 apical setae.
Second maxilliped (Fig. 14H) exopod with 6 apical setae, second segment of endopod now with 1 seta.
Third maxilliped (Fig. 14K) exopod now has 4 apical setae.
First pereiopod (Fig. 14L) small with short, unsegmented exopod without setae, endopod absent.
Second pereiopod as a small bud.
Telson spatuliform with 8 + 8 or 8 + 1 + 8 setae, spine 2 reduced to a hair, median spine absent (Fig. 14B) or present and small (Fig. 14C). The two forms of telson (with or without median spine) are observed in specimens which otherwise agree with one another in all respects.

ZOEA III.   c.l. 1·2–1·4 mm
            t.l. 2·8–3·0 mm

Antennule (Fig. 15D) 2-segmented, terminal segment conical with 2 aesthetascs and 2 setae, peduncle with 3 terminal and 3 lateral setae.
Antenna (Fig. 15C) exopod with 1 spine and 15 setae, endopod with 1 seta.
Maxillule (Fig. 15F) endopod unsegmented with 3 apical setae, basal and coxal endites with 7 and 4 setae respectively.
Maxilla (Fig. 15G) scaphognathite with 9 setae, endopod with 2 setae, bilobed basal and coxal endites with 8 and 5 setae respectively.
First maxilliped (Fig. 15H) unchanged.
Second maxilliped (Fig. 15I) the first segment of the endopod now has 1 seta.
Third maxilliped (Fig. 15J) exopod now with 6 apical setae, endopod still absent.
First pereiopod (Fig. 15K) exopod 2-segmented with 4 apical setae, endopod small, near base of basis.
Second pereiopod (Fig. 15L) small bilobed bud, unsegmented.
Third pereiopod, small rounded bud.
Telson: Two forms of telson are observed: Form A (Fig. 15E) with median spine, spine formula 9 + 1 + 9, spine 2 reduced to a hair, spine 4 the largest and continuous with the telson; form B (Fig. 15B) with or without median spine, spine formula 8 + 1 + 8 or 8 + 0 + 8, spine 2 reduced to a hair, spine 3 the largest and continuous with the telson.
There is some variation in the telson: the median spine is always present in form A but sometimes absent in form B and also the spine placed between the hair-like seta and the largest telson process varies from large to small in A, is absent in B.
Specimens with A or B form of telson do not differ in any other respects.
Uropods (Fig. 15C) exopod with 10–12 setae, endopod with 2–3 setae, basis not yet differentiated.

ZOEA IV.   c.l. 1·2–1·4 mm
           t.l. 2·8–3·0 mm

Carapace (Fig. 16A) now with rostral spine slightly curving upwards.
Antennule (Fig. 16G) with exopod and endopod demarcated from peduncle, exopod fairly large with 2 aesthetascs and 3 setae, endopod small, rounded with 1 small seta, peduncle with 5 terminal setae and 4 lateral ones.

Antenna (Fig. 16H) exopod with 1 spine and 15 setae, endopod with 1 seta.

Mandibles (Fig. 16J) with more teeth on cutting surfaces.

Maxillule (Fig. 16B) endopod with 3 setae, basal and coxal endites with 8 and 4 setae respectively.

Maxilla (Fig. 16C) scaphognathite with 11 setae, endopod small with 2 setae, basal and coxal endites with 10 and 5 setae respectively.

Second maxilliped (Fig. 16F) terminal segment of endopod now with a small lateral seta.

Third maxilliped (Fig. 16K) exopod 2-segmented with 4 terminal setae, endopod very small, rounded, placed near the base of basis.

First pereiopod (Fig. 16M) exopod with 6 apical setae, endopod larger than in previous stage.

Second pereiopod (Fig. 16I) exopod 2-segmented with 4 apical setae, endopod small, placed near base of basis.

Third and fourth pereiopods (Fig. 16L) small bilobed buds.

Fifth pereiopod (Fig. 16L) small rounded bud.

Pleopods, small rounded buds on abdominal segments 2–5.

Telson (Figs 16D, E) two forms of telson are observed both with a median spine: form A with spine formula 10 + 1 + 10, spine 2 hair-like, spine 4 the largest and continuous with the telson, form B with spine formula 9 + 1 + 9, spine 2 hair-like, spine 3 the largest.

Uropods (Fig. 16E) exopod with 1 spine and 14 setae, endopod with 6 setae, basis now differentiated, small.

LAST ZOEA.   c.l. 2·1 mm
　　　　　　t.l. 4·5 mm

Only one specimen of this stage is found. There are probably 1 or 2 stages between this one and stage 4 previously described.

Carapace (Figs. 17A, B) with rostral spine curving upwards. Cervical groove present, still indistinct.

Antennule (Fig. 17D) exopod elongated with 1 terminal seta and with aesthetascs divided into groups of 1, 2 and 2; endopod small with 2 setae, peduncle slender with 3 distal setae near the base of the endopod and 8–9 lateral setae.

Antenna (Fig. 17C) exopod with 1 spine and 23–24 setae, endopod stout without setae, peduncle with 2 spines.

Mandibles (Fig. 16N) with more teeth and spines on cutting surfaces.

Maxillule (Fig. 17I) endopod with 3 apical setae, basal and coxal endites with 11 and 5 setae respectively.

Maxilla (Fig. 17H) scaphognathite with 26 setae, endopod small with 2 setae, basal and coxal endites with 10 and 7 setae respectively.

First maxilliped (Fig. 17E) exopod 2-segmented with 6 terminal setae, endopod 4-segmented with 1, 1, 2, 4 setae, the internal lateral seta has been lost, basis with 4 setae.

Second maxilliped (Fig. 17F) exopod 2-segmented with 6 terminal setae, endopod 4-segmented with 1, 1, 2, 4 setae, the internal lateral seta has been lost, basis unarmed.

Second maxilliped to fourth pereiopod each with a pair of epipods.

Third maxilliped (Fig. 17G) exopod 2-segmented with 6 terminal setae, endopod now well developed, elongated, placed near the base of basis, basis unarmed.

First pereiopod (Fig. 17K) exopod 2-segmented with 6 terminal setae, endopod well developed, 5-segmented, cheliform, unarmed, placed near base of basis which is also unarmed.

Second and third pereiopods (Figs 17J, M) exopods 2-segmented with 6 apical setae, endopods 5-segmented, unarmed, placed near the base of basis, basis also unarmed.

Fourth pereiopod (Fig. 17L) exopod 2-segmented, endopod 5-segmented, both unarmed, endopod placed near base of basis, basis unarmed.

Fifth pereiopod (Fig. 17N) exopod absent, endopod 5-segmented, both endopod and basis unarmed.

Second to fifth pleopods (Fig. 16O) exopods and endopods lanceolate, unarmed, endopods each with a small internal lateral bud.

Uropod (Fig. 17O) exopod with a small spine and 19 setae, endopod with 17 setae, basis well differentiated.

Telson (Fig. 17O) nearly rectangular in shape with posterior base slightly broader than anterior, spine formula 9 + 1 + 9, spine 2 the largest and continuous with the telson, hair-like seta lost.

Discussion

The affinities of the *Axianassa* sp. larvae described above to some other Thalassinids are discussed below under 3 headings.

1. The affinities to Menon's Madras larvae

There are many similarities between the present *Axianassa* sp. and the larvae from the Madras plankton described by Menon (1933) as belonging to the Upogebiinae. These are:

(*a*) The general body form and rostrum.

(*b*) Presence of a pair of lateral spines on the 5th abdominal segment and absence of spines or hooks on any others.

(*c*) The shape of the telson and appendages in all larval stages.

(*d*) The first pair of pereiopods is cheliform in the late larval stages.

(*e*) Presence of epipods on maxillipeds 2, 3 and pereiopods 1–4 in the late larval stages.

(*f*) As a small bud is present on the endopod of the pleopods in the last stage of the Mexican species, the postlarvae probably have an *appendix interna* on the pleopods as in Menon's material.

The differences between the two species are as follows:

(*a*) In Menon's material the median spine on the telson does not appear until stage 5 whilst in the Mexican species it is present from stage 2. Nevertheless, its presence varies, as in the same stage it may be missing in some specimens.

(*b*) In stages 3 and 4 the telson of Menon's material resembles the form B of the Mexican species, except for the presence of a median spine. The spinulation of the telson posterior border is the same in both materials. On the contrary, in stage 5 which is considered to be the last in Menon's material, a median spine appears on the posterior border of the telson, and on either side 5 spines are found between it and the largest telson process. In the Mexican larvae there are 7 spines instead.

(*c*) As mentioned by Gurney (1938), Menon's species appears to lack the sickle-shaped left mandible which is present in the Mexican larvae. It is possible that Menon overlooked the left mandible while the right one figured by him is very similar to that of the Mexican species.

(*d*) Menon's material also differs from that of *Axianassa* sp. by not having an exopod on the 4th pereiopod.

It is difficult to know whether the 5th zoea described by Menon is actually the last larval stage of his species. As mentioned above, the Mexican *Axianassa* sp. probably goes through at least 6 or 7 stages before metamorphosis. Its last stage resembles Menon's stage 5 in having all pereiopods well developed and epipods on maxillipeds 2, 3 and pereiopods 1–4. It seems more advanced in having a well developed antennule with aesthetascs divided into groups of 1, 2, 2, a maxilla scaphognathite with more setae and a bare proximal extension. It also has larger pleopods with well differentiated basis and a bud on the endopods, a telson approximating a rectangular shape and more setae on both the exopod and the endopod of the uropods.

As described above, the development of the pereiopods is retarded in *Axianassa* sp. and the 4th leg remains as a bud throughout many stages. Its exopod is probably only differentiated—and yet unarmed—in the last larval stage. This suggests that Menon's species would have to go through more than 5 stages before metamorphosis and that only in its last zoea, would it have developed the exopod of the 4th pereiopod.

On a whole, similarities between Mexican *Axianassa* sp. and Menon's material are evident and they are, with little doubt, closely related. One important feature of this relationship is the presence, in the last stage, of a small bud on all pleopods in the Mexican larvae which would have probably given rise later to an *appendix interna* as observed in the postlarvae of Menon's species. If this is the case these two species could satisfactorily be placed within the same genus; nevertheless, as the exopod on pereiopod 4 is present in one species and apparently absent in the other, this view is a tentative one.

2. *The affinities to the Upogebiidae*

Can the larvae of *Axianassa* sp. from the gulf of Mexico and also those from Madras described by Menon be identified as upogebiid?

These two species share many common characters with the Upogebiidae which will be discussed later in this work. They differ in the following features:

(*a*) The higher number of larval stages.

(*b*) The shape of the maxillule and maxilla, especially the unsegmented endopod of the former and the very small endopod of the latter.

(*c*) The asymmetrical mandibles the left of which is sickleshaped.

(*d*) The very rudimentary endopod of the third maxilliped.

(*e*) The retarded development of the endopod of the third maxilliped as well as that of all pereiopods.

(*f*) The presence of epipods on maxillipeds 2, 3 and pereiopods 1–4.

(*g*) The presence of an exopod on pereiopod 4 in *Axianassa*.

(*h*) The possible presence of an *appendix interna* on the pleopods in the postlarval stage.

(*i*) The absence of an anal spine.

Gurney (1938), while discussing the position of Menon's larval material from Madras, stated that the presence of epipods on the legs and of an *appendix interna* on the pleopods in the postlarval stage excluded this material from the Upogebiidae. On the other hand, the presence of epipods on legs, of an exopod on leg 4, and especially the presence of the asymmetrical mandibles reveal evidence of a relationship to *Axianassa* sp. with the Laomediidae.

3. *The affinities to the Laomediidae*

Five genera are known for the adults of the Laomediidae at present. They are: *Laomedia* de Haan, *Naushonia* Kingsley, *Jaxea* Nardo, *Axianassa* Schmitt and *Laurentiella* Le Loeuff & Intes. The larvae have been described for *Laomedia* (Sakai & Miyake, 1964; Yaldwyn & Wear, 1972), *Naushonia* (Gurney, 1938; Gurney & Lebour, 1939; Dakin & Colefax, 1940; Goy & Provenzano, 1978), *Jaxea* (Claus, 1884; Cano, 1891; Bouvier, 1914; Caroli, 1924; Gurney, 1924, 1938; Tattersall, 1938; Dakin & Colefax, 1940; Wear & Yaldwyn, 1966). The first larval stage of *Naushonia crangonoides* Kingsley was collected from plankton and the following 6 stages as well as the first postlarva were obtained from laboratory rearing (Goy & Provenzano, 1978). For the remaining laomediid larvae so far known, descriptions have been based on plankton material.

Mention must be made of the first larval stage of *Laomedia astacina* de Haan described by Sakai & Miyake (1964) and by Yaldwyn & Wear (1972). The larvae described in the former paper are evidently laomediid and it would seem, as Goy & Provenzano (1978) suggested, that the account given by the latter authors are probably of an *Upogebia* species. Nevertheless, *Upogebia* larvae so far known constitute a very homogenous group and those described by Yaldwyn & Wear (1972) differ by the shape of their antennal scale, of their telson and mandibles. The problem can only be settled by new rearing experiments of the species. In the present work, those described by Sakai & Miyake (1964) are considered as the true larvae of *Laomedia astacina*.

Axianassa sp. can be assigned to the Laomediidae as it resembles known larvae of the family as follows:

(*a*) The number of larval stages is 6 or 7.

(*b*) The antennal scale is not segmented, the antennal endopod has 3 apical setae in stage 1.

(*c*) The mandibles are asymmetrical, the left of which is sickle-shaped.

(*d*) The endopod of the maxillule is unsegmented.

(*e*) The endopod of the maxilla is very reduced and the scaphognathite, in late stages, has an proximal extension devoid of setae.

(*f*) Maxillipeds 1 and 2 have the basis long, cylindrical and the setae of the endopods small and delicate.

(*g*) The endopod of maxilliped 3 is rudimentary and placed low on the basis.

(*h*) The development of the endopods of the maxilliped 3 and all pereiopods is retarded.

(*i*) The endopods of the pereiopods remain in most cases unsegmented and inserted low on the basis.

(*j*) There are exopods on pereiopods 1–4, the exopod on pereiopod 4 is often rudimentary and not differentiated until the late stages.

Table 3   Differences between laomediid larvae of the first and the second group

	First group	Second group
Total length (mm) stage 1	*Naushonia* sp.: 2·2	Menon's species: 1·8
	Jaxea sp.: 4·5	
	(Dakin & Colefax, 1940)	Gurney species: 2·4
	Laomedia astacina: 3·2	*Axianassa* sp.: 2·1
	(Sakai & Miyake, 1964)	
	Jaxea novaezealandiae: 4	
	(Wear & Yaldwyn, 1966)	
	Naushonia crangonoides: 2·6	
	(Goy & Provenzano, 1978)	
Total length (mm) Late stages	*Naushonia* sp.: 7	Menon's species: 4·25
	Jaxea sp.: 15	(stage 5)
stage 6	*J. novaezealandiae*: 13·8–15·2	Gurney's species: 5·7
	N. crangonoides: 7·8–8·5	*Axianassa* sp.: 4·5
		(stage 6 or 7)
'Neck' region	more or less elongated	non elongated
Rostrum	curved	straight, upturned
	Exceptions are a species of	
	Jaxea (Gurney 1938 : 334)	
	devoid of rostrum and	
	L. astacina (Sakai & Miyake,	
	1964) with an inconspicuous	
	one.	
Antennular peduncle	2-segmented in late stages	unsegmented
Apical spine on antennal scale	absent	present
Procurved pleural hooks on abdominal segments	present at least on segments 2–5 except in a species of *Naushonia* (Gurney, 1938)	present in Gurney's species, absent in others
A pair of lateral spines on abdominal segment 5	absent	present
Appendix interna on pleopods in postlarval stage	presumably absent	presumably present
Median spine on telson in late stages	absent	present
Lateral spines on exopod of uropods in late stages	present in *Jaxea* only	present

(*k*) The telson approximates a triangular shape in stage 1 with a median hollow and a spine formula of 7 + 7, spine 2 is reduced to a hair. There is no median spine.

(*l*) The anal spine is absent.

With the inclusion of the species assigned to *Axianassa* and probably also of Menon's species in the Laomediidae, it is possible to divide the known larvae of this family into 2 groups. To the first group can be assigned all larvae so far described belonging to genera *Laomedia, Naushonia* and *Jaxea.* Into the second are placed the *Axianassa* sp., Menon's species and also a species described by Gurney (1938 : 337) as a laomediid.

Characters separating the two groups are summarized in Table 3.

The most apparent features distinguishing the larvae of the two groups are probably the 'neck' region and the rostrum. This 'neck' region, extending between the mouth and the base of the rostrum, is more or less elongated in the larvae of the first group and normal in the second. On the other hand known larvae of *Jaxea* and *Naushonia* have a small and curved rostrum whilst the three species of the second group have a fairly large one, that is straight and upturned. Two further important differences can be added, (1) the presence or absence of an *appendix interna* on the postlarval pleopods, (2) a median spine on the telson. These features make the separation between the two groups even more distinct. The Mexican larval species here studied can therefore be assigned to neither genera of the first group, i.e. *Laomedia, Jaxea* or *Naushonia.*

Could it belong to genus *Axianassa* or *Laurentiella* the larvae of which are not yet known? The greatest disagreement here is the suggested presence of an *appendix interna* on the pleopods of the post-larvae of the Mexican species that is absent in the known adults of both *Axianassa* and *Laurentiella.* The adult of this Mexican species, although belonging to the Laomediidae, may show important differences from those of *Laomedia, Jaxea* and *Naushonia.* It is possible that the postlarvae possess an *appendix interna* on the pleopods that may disappear in the adult. Nevertheless, as the adults of genus *Axianassa* have been found in the neighbouring area, this material is provisionally identified as *Axianassa* sp. until its adult form is known.

C. The relationships between larvae of the Laomediidae, Upogebiidae and adults of the Glypheidae

With the present knowledge of the larvae of the Laomediidae, certain characters can no longer be considered as holding good for the whole family. These are:

(*a*) The lengthening of the 'neck' region.

(*b*) The pleura of some or all abdominal segments drawn into hooks curved forwards.

(*c*) The absence of a median spine on the telson.

(*d*) The absence of an *appendix interna* on the pleopods.

As discussed above, the larvae of the Laomediidae can be divided into two groups and the above features apply only to the first one. Larvae of the first group have a body shape that clearly distinguishes them from all other thalassinids while those of the second group show a general resemblance to *Upogebia.* The possible relationship between the larvae of the Laomediidae with the adults of the Glypheidae on one hand and with the larvae of the Upogebiidae on the other will be discussed below.

1. Several authors (Burkenroad, 1963; Glaessner, 1969; Forest & de Saint Laurent, 1975) pointed out the relationships between the Glypheidea and the Thalassinidea. The former are a group of crustaceans that flourished in the Jurassic and generally thought to have become extinct by the Eocene but in fact have survived to the Recent. A species, *Neoglyphea inopinata* of the family Glypheidae has been described (Forest & de Saint Laurent, 1975, 1976). The holotype measures 11·5 mm in total length with a triangular curved rostrum, a long epistoma, an elongated area between the mouth and the antennal basis, an *appendix interna* on the pleopods and a suture on the exopod of the uropods. Laomediid larvae of the first group are also provided with a curved rostrum and an elongated 'neck' area and show a resemblance to *Neoglyphea inopinata* in the anterior part of their body; this resemblance is

more pronounced in those belonging to *Naushonia,* the 'neck' region of which is only slightly elongated; postlarve of the second group, on the other hand share with *Neoglyphea* the presence of an *appendix interna* on the pleopods. This perhaps suggests a parental relationship between Glypheidae and Laomediidae and that laomediid larvae show, in their ontogeny, a recapitulation of ancestral characters. It can be noted that adults of the Laomediidae, except *Axianassa,* have a suture either on the exopod or both exopod and endopod of the uropods and those of *Naushonia* (Goy & Provenzano, 1979) have a first pereiopod somewhat similar to that of *Neoglyphea inopinata* (Forest & de Saint Laurent, 1976). Further examination of *N. inopinata* needs to be made to provide information on the above suggestion. Apparently, there are no similarities between its mouth appendages and those of either larval or adult laomediids (de Saint Laurent, personal communication) and its mandibles are symmetrical.

2. Affinities between larvae of the Laomediidae and the Upogebiidae were pointed out by Gurney (1938) who placed both families in an anomuran group with these common characters:

(*a*) Rostrum small and round.
(*b*) Abdomen without dorsal spines.
(*c*) Median spine on telson small or absent, always absent in stage 1.
(*d*) Exopods on leg 3 or legs 3 and 4, never on leg 5.
(*e*) Endopod of maxilliped 3 rudimentary and seated at base of basipod.

In addition, in biramous pereiopods the endopods have also shifted near the base of the basipod.

These above features hold good for all laomediid and upogebiid larvae known at present. Nevertheless, compared with the Upogebiidae, laomediid larvae of the first group differ on account of their lengthened neck area, their long and delicate body, their rostrum and their telson shape. A closer relationship with the Upogebiidae can be found in the second group of laomediid larvae. These, in fact, possess a number of characters which separate them from larvae of the first group and bring them near those of the Upogebiidae. They are listed in Table 3 and summarized below:

(*a*) The non-elongated neck region.
(*b*) The rostrum fairly large, straight and upturned.
It is this shortening of the neck region and the form of the rostrum which contribute mainly to the general resemblance of the second group of the Laomediidae and the Upogebiidae.
(*c*) The unsegmented antennular peduncle.
(*d*) The presence of an apical spine on the antennal scale.
(*e*) The presence of a pair of large lateral spines on abdominal segments 5.
Only a small group of upogebiid larvae, namely *U. affinis* and Mexican *Upogebia* spp. A and B previously described share this character. They probably constitute a group of *Upogebia* larvae the most closely related to the Laomediidae.
(*f*) The presence of a median spine on the telson in the late stages.
In *Axianassa* sp. the median spine appears on the telson in stage 2 as in *Upogebia.* Nevertheless, as described above, there is variation in this respect, that is the median spine can be present or absent in specimens of the same stage.
(*g*) In stage 1 all laomediid larvae have a similar triangular telson shape with a median hollow. Later, the telson in *Axianassa* sp. and other laomediid larvae of the second group has a median spine and a shape definitely approximating that of *Upogebia.*
(*h*) In stage 1 all known laomediid and upogebiid larvae (see Table 3 and Ngoc-Ho, 1977) are rather small with a total length ranging between 2–4 mm. In later stages, while laomediid larvae of the first group reach a much larger size (t.l. 7–15 mm), those of the second group remain small (t.l. 4–6 mm) and resemble the larvae of *Upogebia* (t.l. 3–5 mm).

The last 3 characters mentioned seem to suggest an intermediate position of laomediid larvae of the second group between those of the first and the Upogebiidae. It is interesting to note that while the larvae of *Axianassa* sp. and related species are indisputably laomediid by

the shape and spinulation of their appendages (their mouth appendages especially), they show a general external resemblance to the Upogebiidae by their size, their neck region, their rostrum and telson shape.

Although Gurney (1938) suggested the placing of the Laomediidae and Upogebiidae in the same anomuran group of the Thalassinidea, relationships between adults and larvae of these two families are not at all clear (de Saint Laurent, 1979). The present study of *Axianassa* sp. and its relatives clearly demonstrates that these larvae possess combined characters of both families. However, the postlarvae of the second group of the Laomediidae possibly have an *appendix interna* on the pleopods and this feature separates them from both the Laomediidae of the first group and the Upogebiidae. It is not known whether any relationships exist between them and the Callianassidae or Axiidae, two thalassinid families which also share this character.

Acknowledgements

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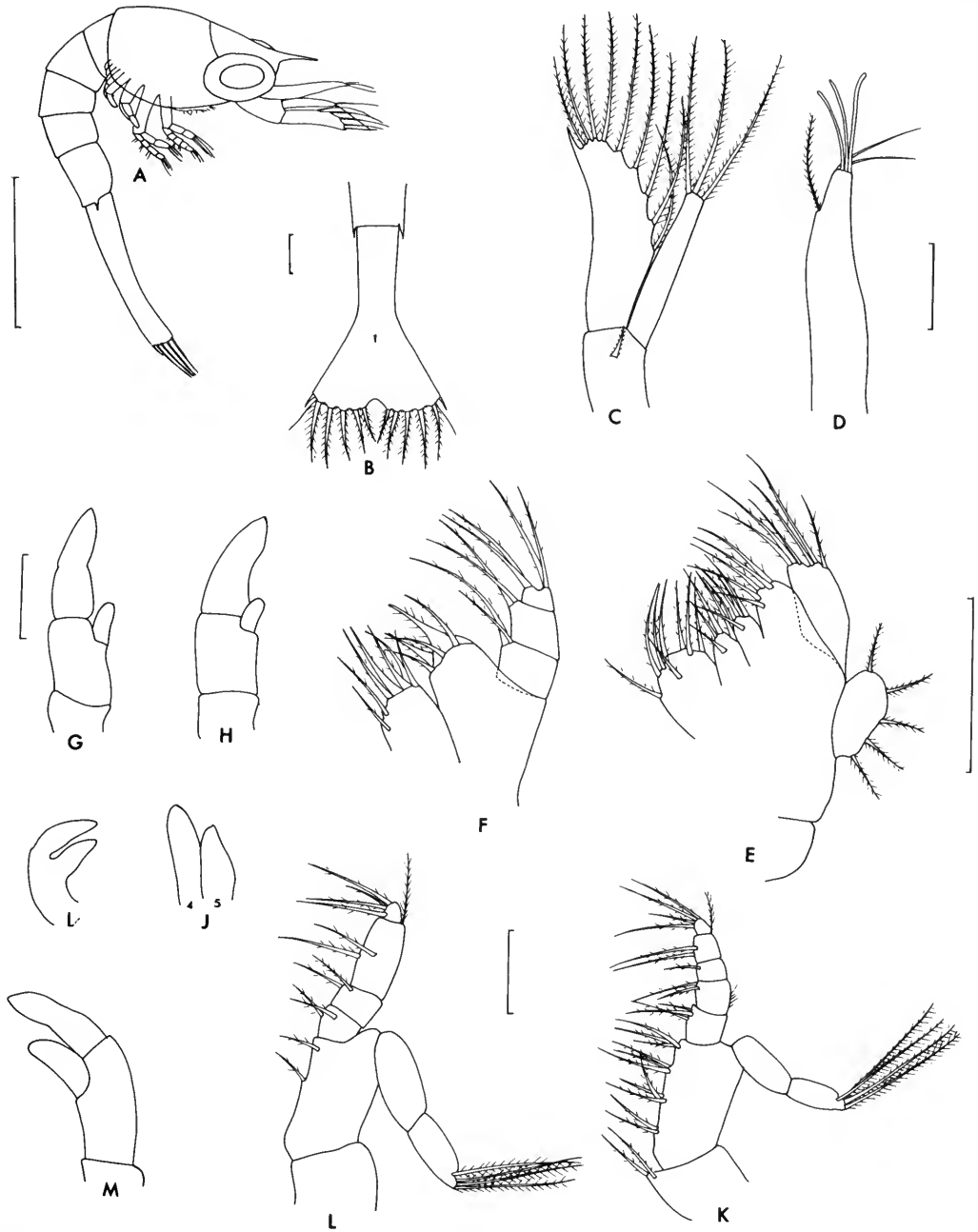
Fig. 1 *Upogebia* sp. A. Zoea I. A, lateral view; B, telson in dorsal view; C, antenna; D, antennule; E, maxilla; F, maxillule; G, pereiopod 1; H, pereiopod 2; I, pereiopod 3; J4 and 5, pereiopods 4 and 5; K, first maxilliped; L, second maxilliped; M, third maxilliped. Scale. 0·5 mm: A; 0·1 mm: B–M.
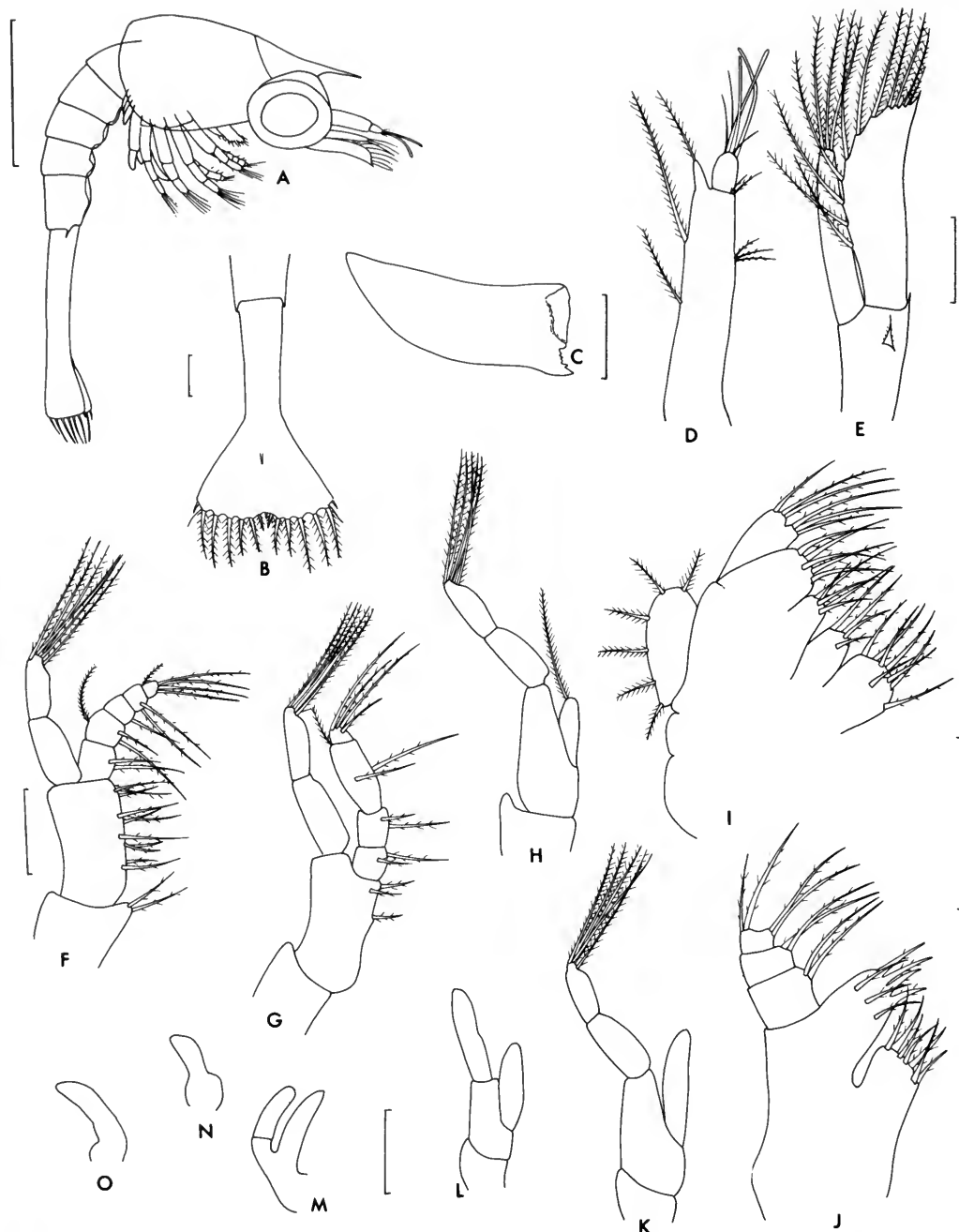
Fig. 2 *Upogebia* sp. A. Zoea II. A, lateral view; B, telson in dorsal view; C, mandible; D, antennule; E, antenna; F, first maxilliped; G, second maxilliped; H, third maxilliped; I, maxilla; J, maxillule; K, L, M, N, O, pereiopods 1, 2, 3, 4, 5 respectively. Scale. 0·5 mm: A; 0·1 mm: B–O.
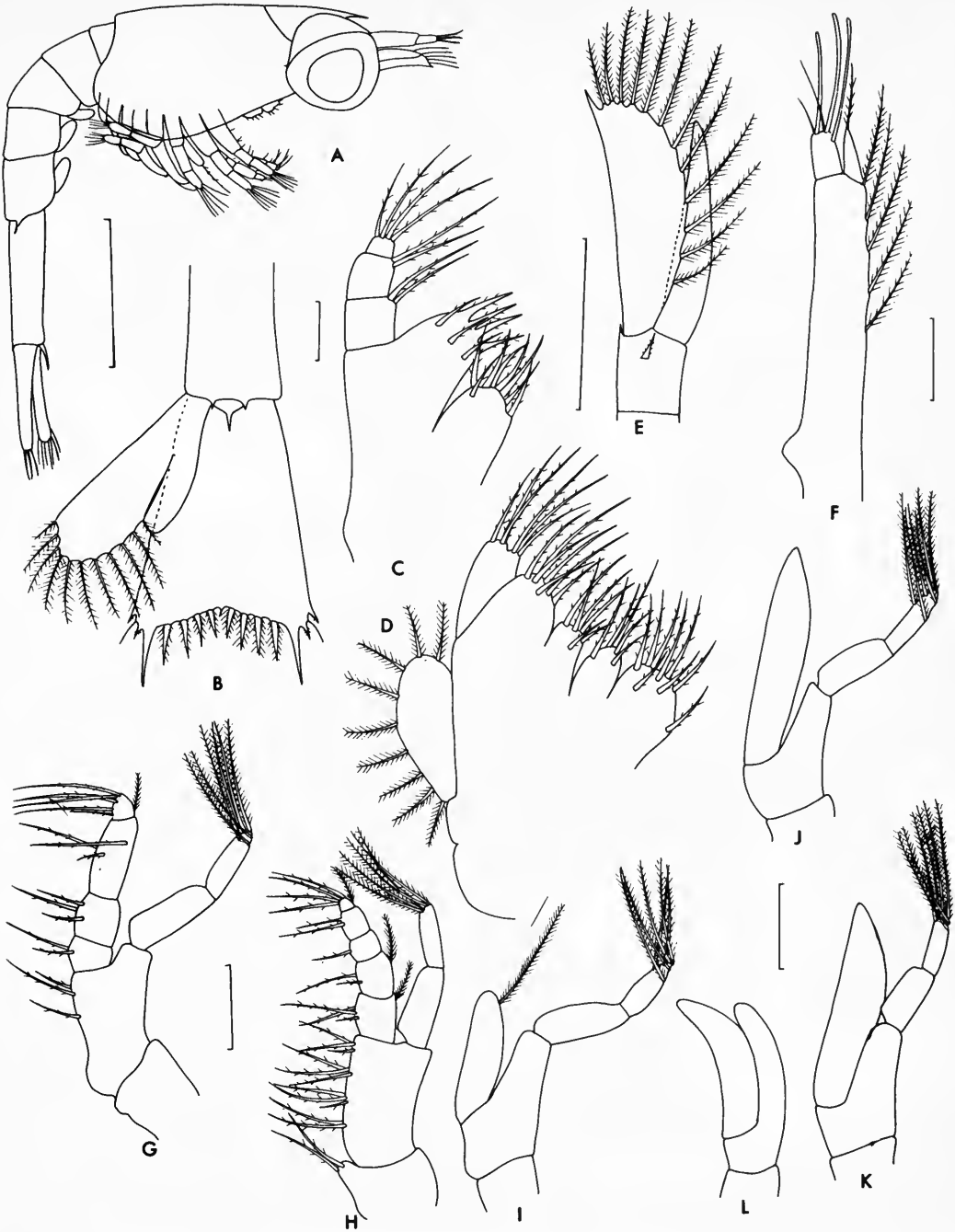
Fig. 3 *Upogebia* sp. A. Zoea III. A, lateral view; B, telson and uropods in dorsal view; C, maxillule; D, maxilla; E, antenna; F, antennule; G, second maxilliped; H, first maxilliped; I, third maxilliped; J, K, L, pereiopods 1, 2 and 3 respectively. Scale. 0·5 mm: A; 0·1 mm: B–L.
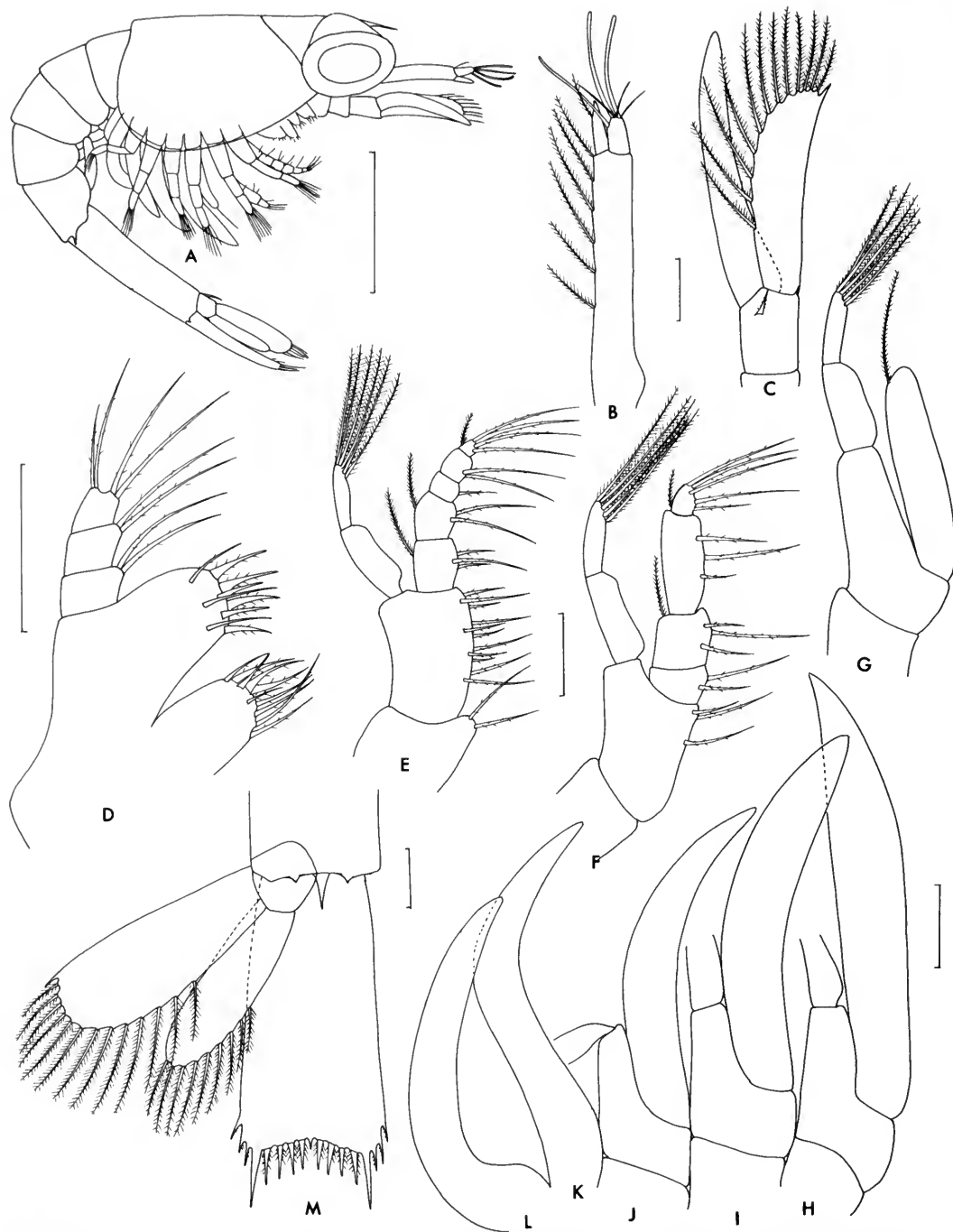
Fig. 4 *Upogebia* sp. A. Zoea IV. A, lateral view; B, antennule; C, antenna; D, maxillule; E, F, G, first, second and third maxillipeds respectively; H, I, J, K, L, pereiopods 1, 2, 3, 4 and 5 respectively; M, telson and uropods in dorsal view. Scale 0·5 mm; A; 0·1 mm: B–M.

Fig. 5 *Upogebia* sp. A. Zoea V. A, lateral view; B, telson and uropods in dorsal view; C, mandible; D, maxillule; E, maxilla; F, antenna; G, antennule; H, third maxilliped; I, first maxilliped; J, second maxilliped; K, L, M, N, O, pereiopods 1, 2, 3, 4 and 5 respectively; P2 and 4, pleopods 2 and 4. Scale. 0·5 mm: A; 0·1 mm: B–P.
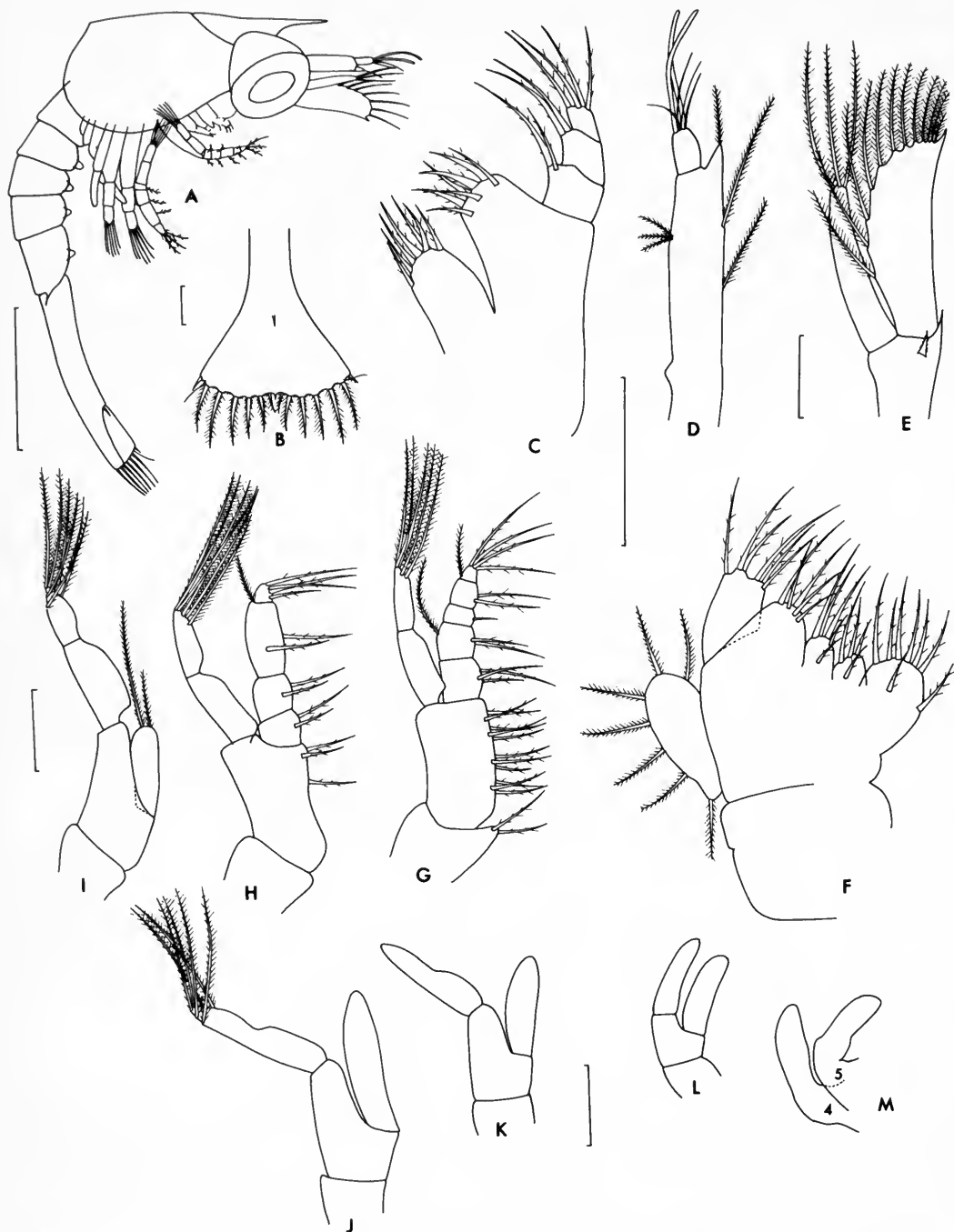
Fig. 6 *Upogebia affinis* (Say). Zoea II. A, lateral view; B, telson in dorsal view; C, maxillule; D, antennule; E, antenna; F, maxilla; G, H, I, first, second and third maxilliped respectively; J, K, L, M4 and M5, pereiopods 1, 2, 3, 4 and 5 respectively. Scale. 0·5 mm: A; 0·1 mm: B–M.
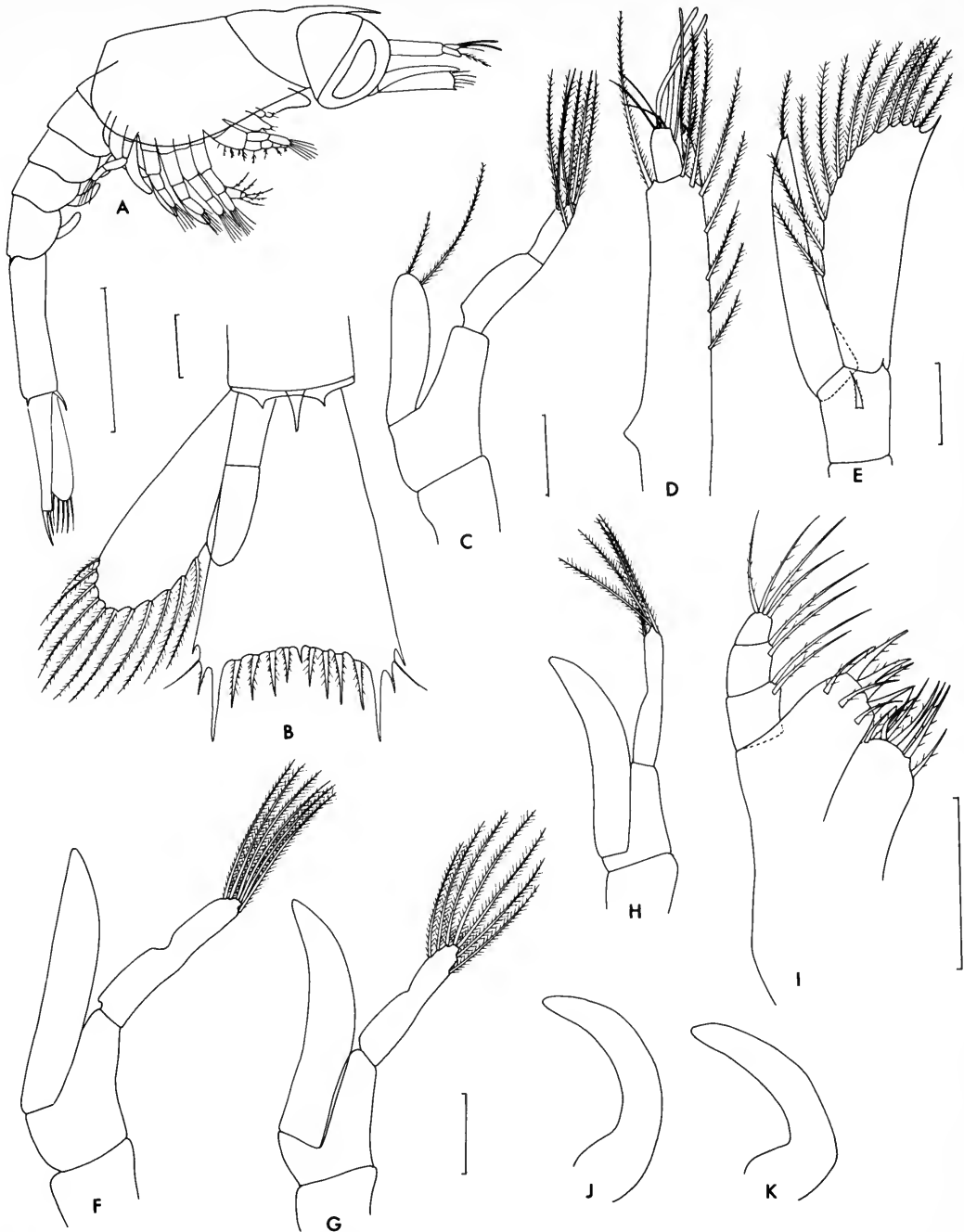
Fig. 7 *Upogebia affinis* (Say). Zoea III. A, lateral view; B, telson and uropods in dorsal view; C, third maxilliped; D, antennule; E, antenna; F, G, H, pereiopods 1, 2 and 3 respectively; I, maxillule; J, K, pereiopods 4 and 5. Scale. 0·5 mm: A; 0·1 mm: B–K.
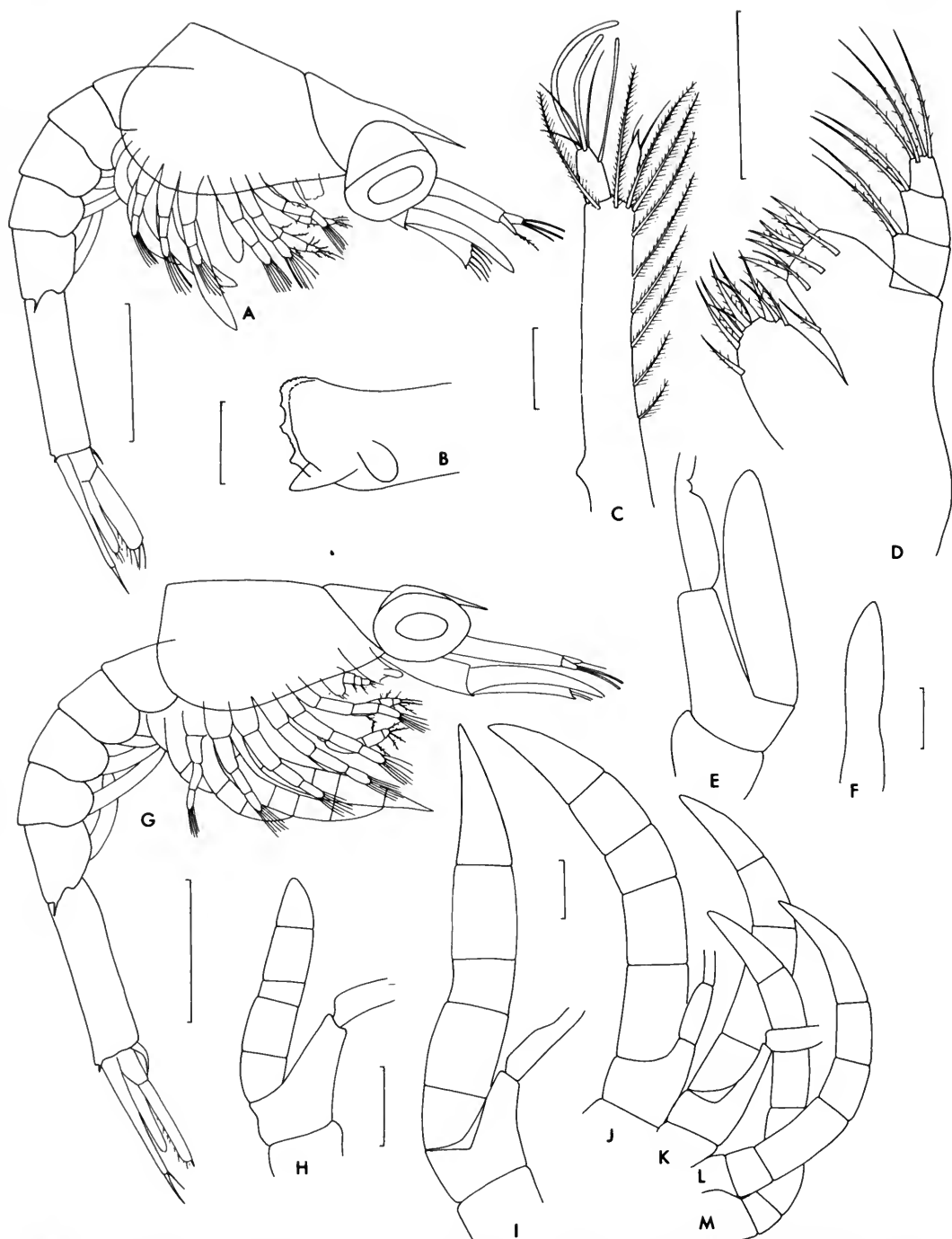
Fig. 8 *Upogebia affinis* (Say). Zoea IV (A–F) and V (G–M). A, Zoea IV larva in lateral view; B, mandible; C, antennule; D, maxillule; E, third maxilliped; F, pleopod 2; G, zoea V larva in lateral view; H, third maxilliped; I, J, K, L, M, pereiopods 1, 2, 3, 4 and 5 respectively. Scale. 0·5 mm: A, G; 0·1 mm: B–F, H–M.
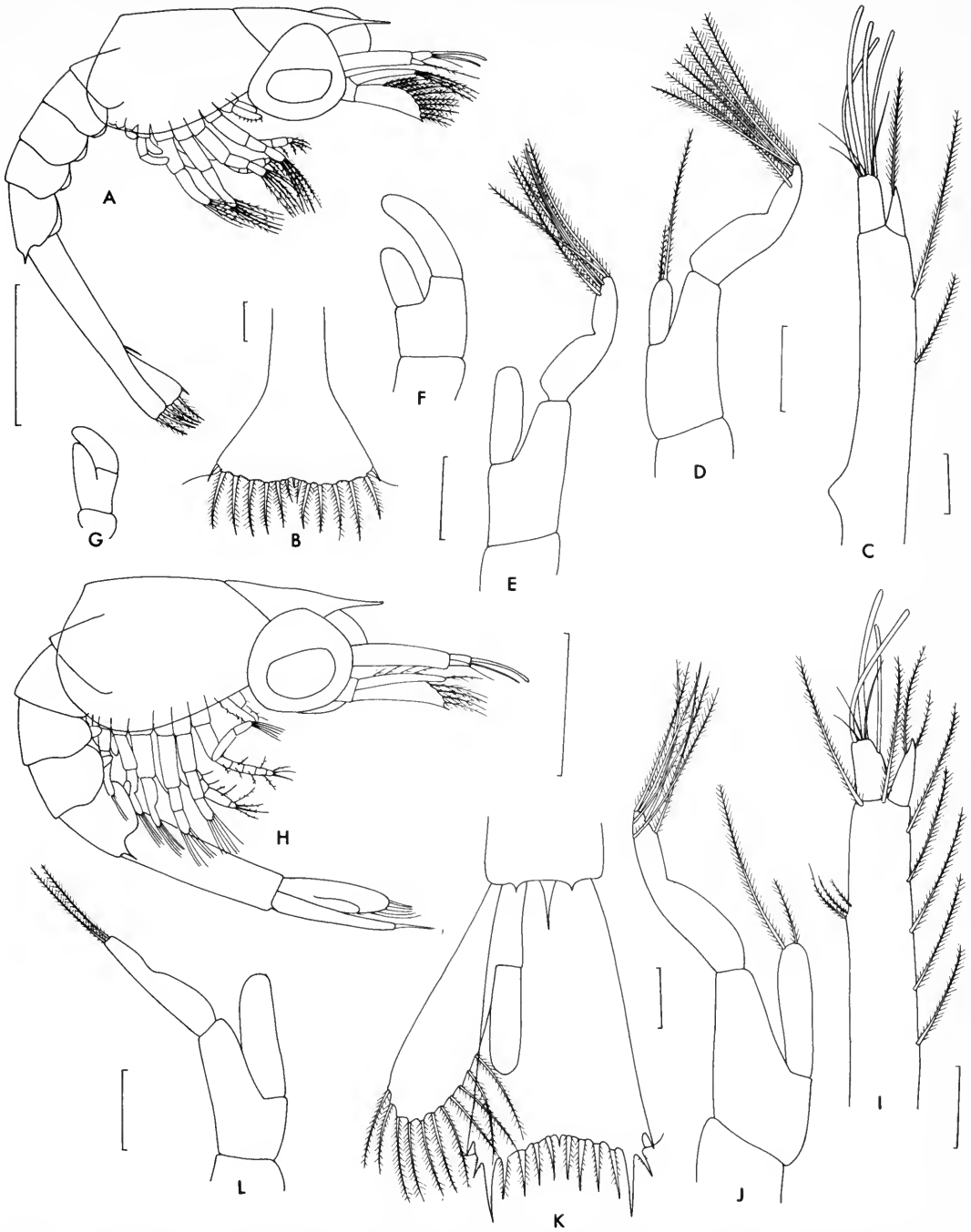
Fig. 9 *Upogebia* sp. B. Zoea II (A–G) and III (H–L). A, zoea II larva in lateral view; B, telson in dorsal view; C, antennule; D, third maxilliped; E, F, G, pereiopods 1, 2 and 3 respectively; H, zoea III larval in lateral view; I, antennule; J, third maxilliped; K, telson and uropods in dorsal view; L, pereiopod 3. Scale. 0·5 mm: A, H; 0·1 mm: B–G, I–L.
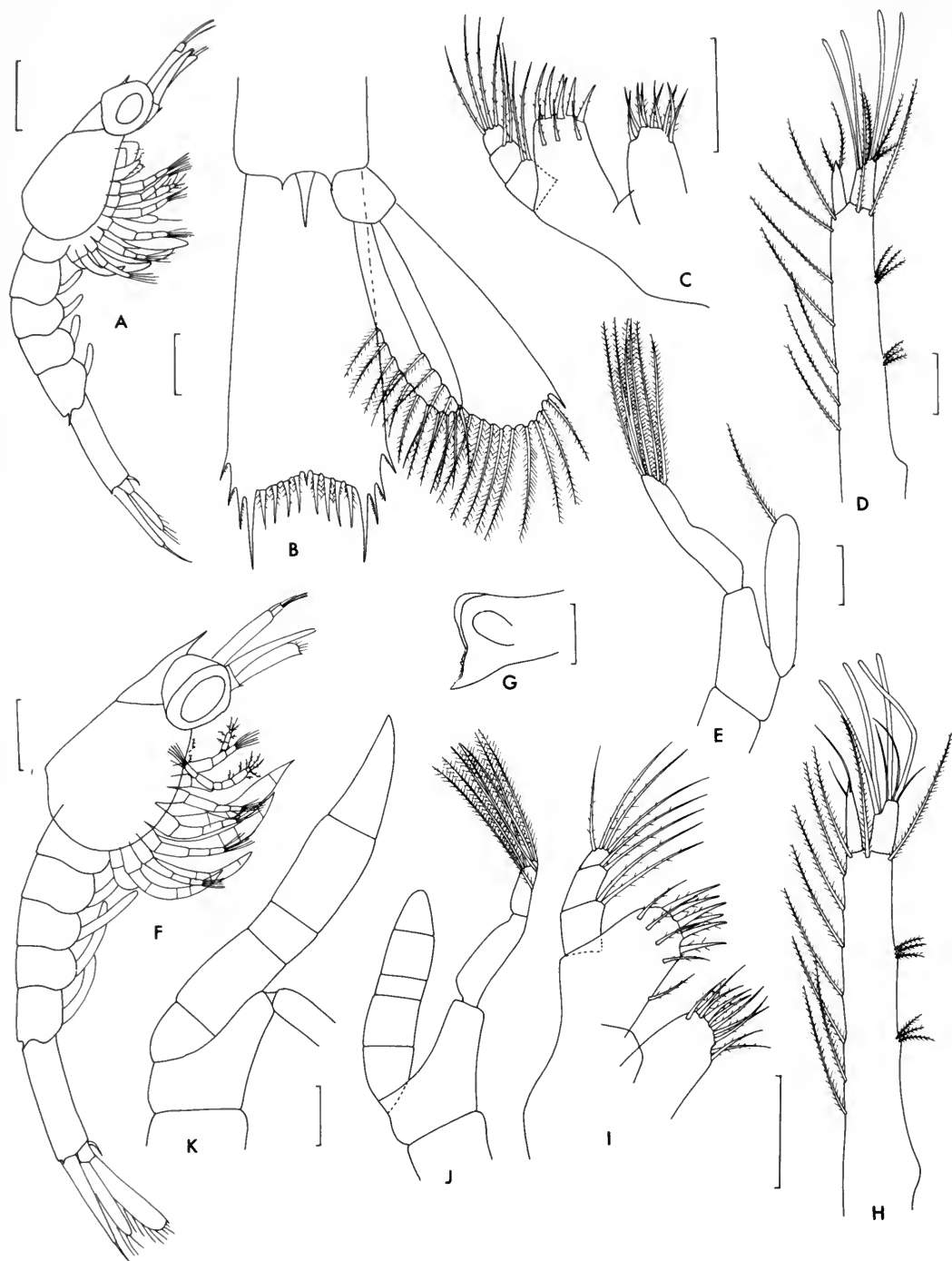
Fig. 10 *Upogebia* sp. B. Zoea IV (A–E) and V (F–K). A, zoea IV larva in lateral view; B, telson and uropods in dorsal view; C, maxillule; D, antennule; E, third maxilliped; F, zoea V larva in lateral view; G, mandible; H, antennule; I, maxillule; J, third maxilliped; K, pereiopod I. Scale. 0·5 mm: A, F; 0·1 mm: B–E, G–K.
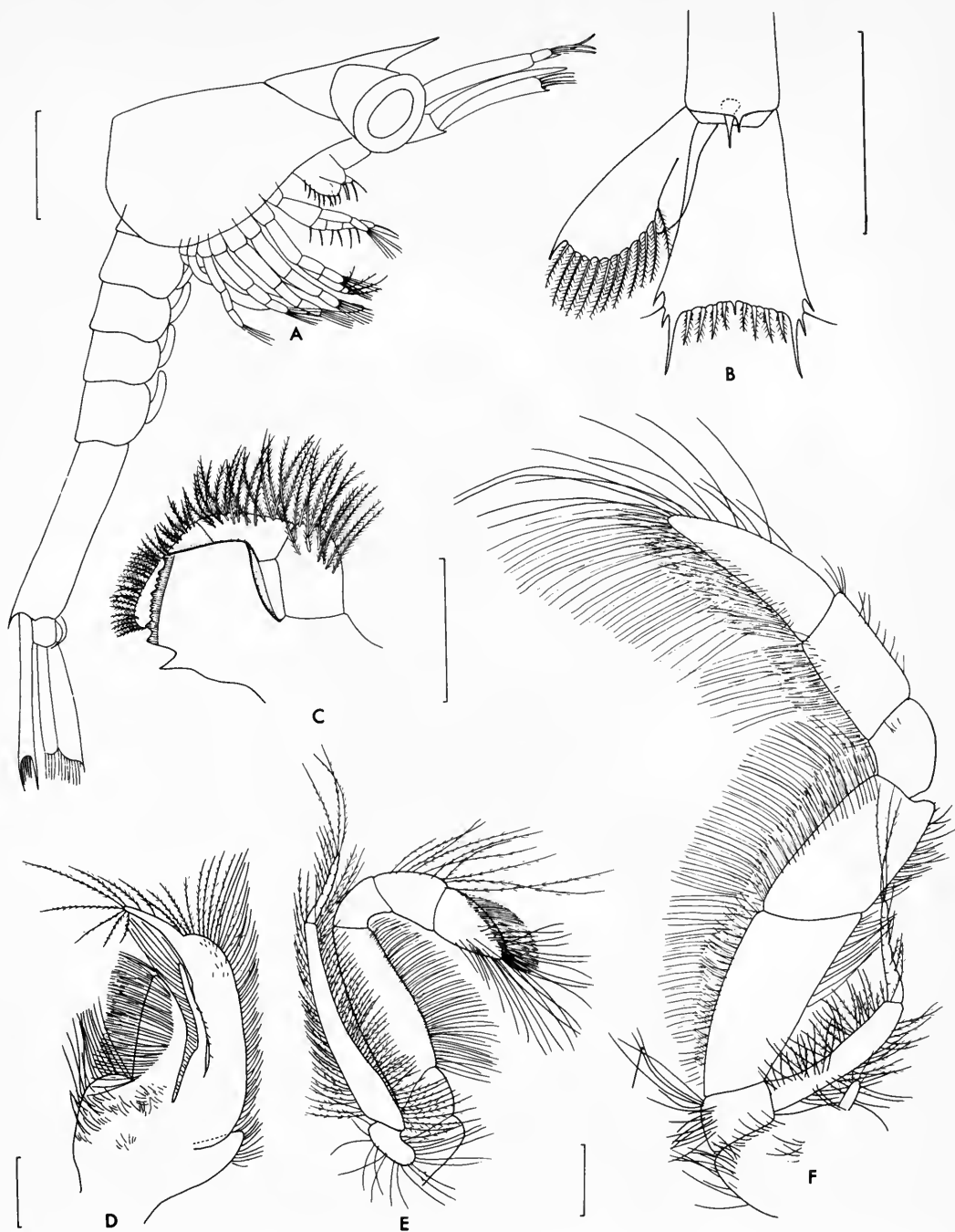
Fig. 11 *Upogebia* larvae and adults. A, B, *Upogebia* sp. larvae from the Great Barrier Reef: A, zoea IV or V in lateral view; B, zoea III, telson and uropods in dorsal view. C–F: *U. issaeffi* adult: C, mandible; D, E, F, first, second and third maxillipeds respectively. Scale. 0·5 mm: A, B; 0·1 mm: C–F.
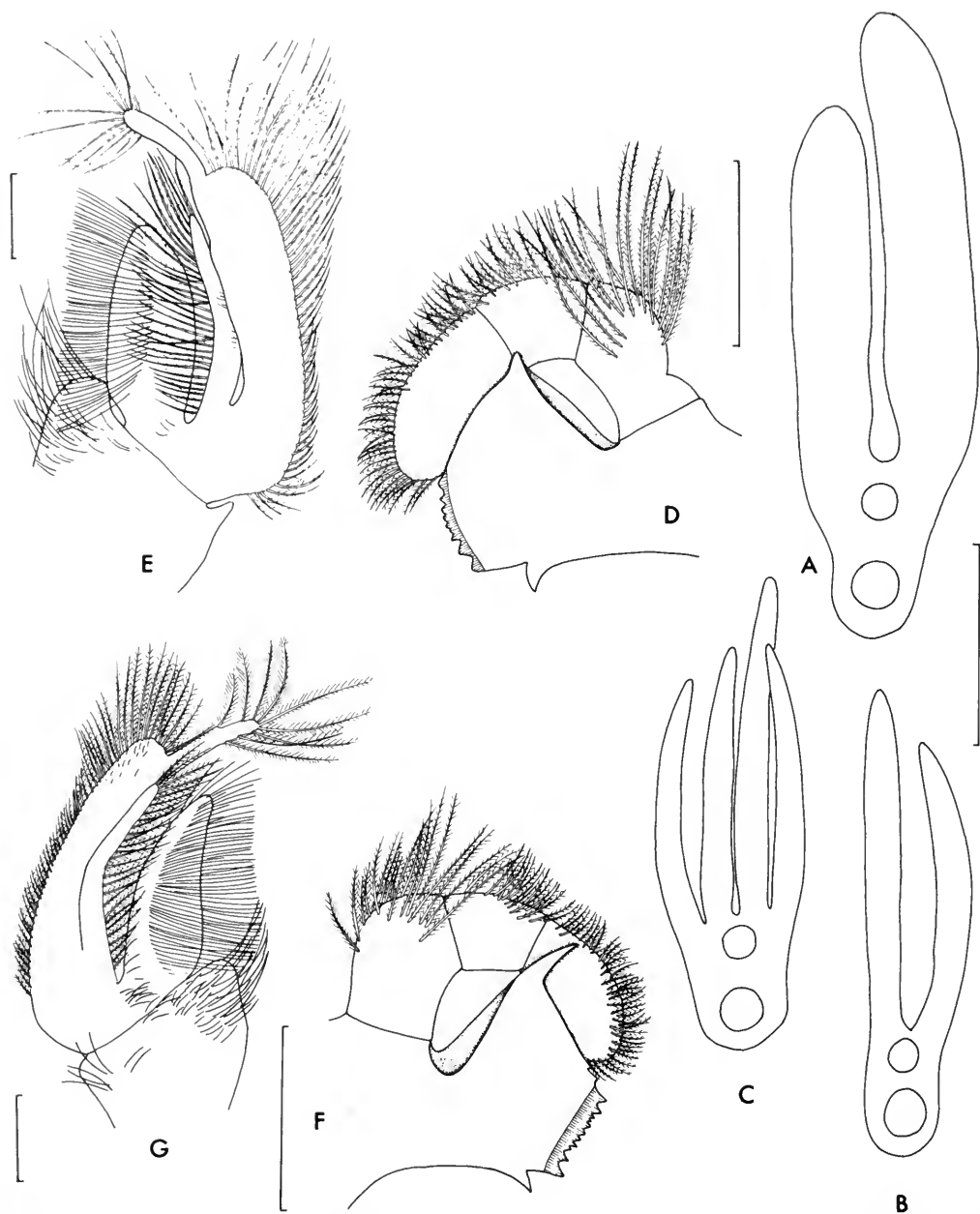
Fig. 12 *Upogebia* adults. A–C: different types of arthrobranchs: A, type A in *U. issaeffi*; B, type B in *U. savignyi*; C, type C in *U. stellata*; D, E, *U. africana*, mandible and first maxilliped; F, G, *U. deltaura*, mandible and first maxilliped. Scale: 1 mm.
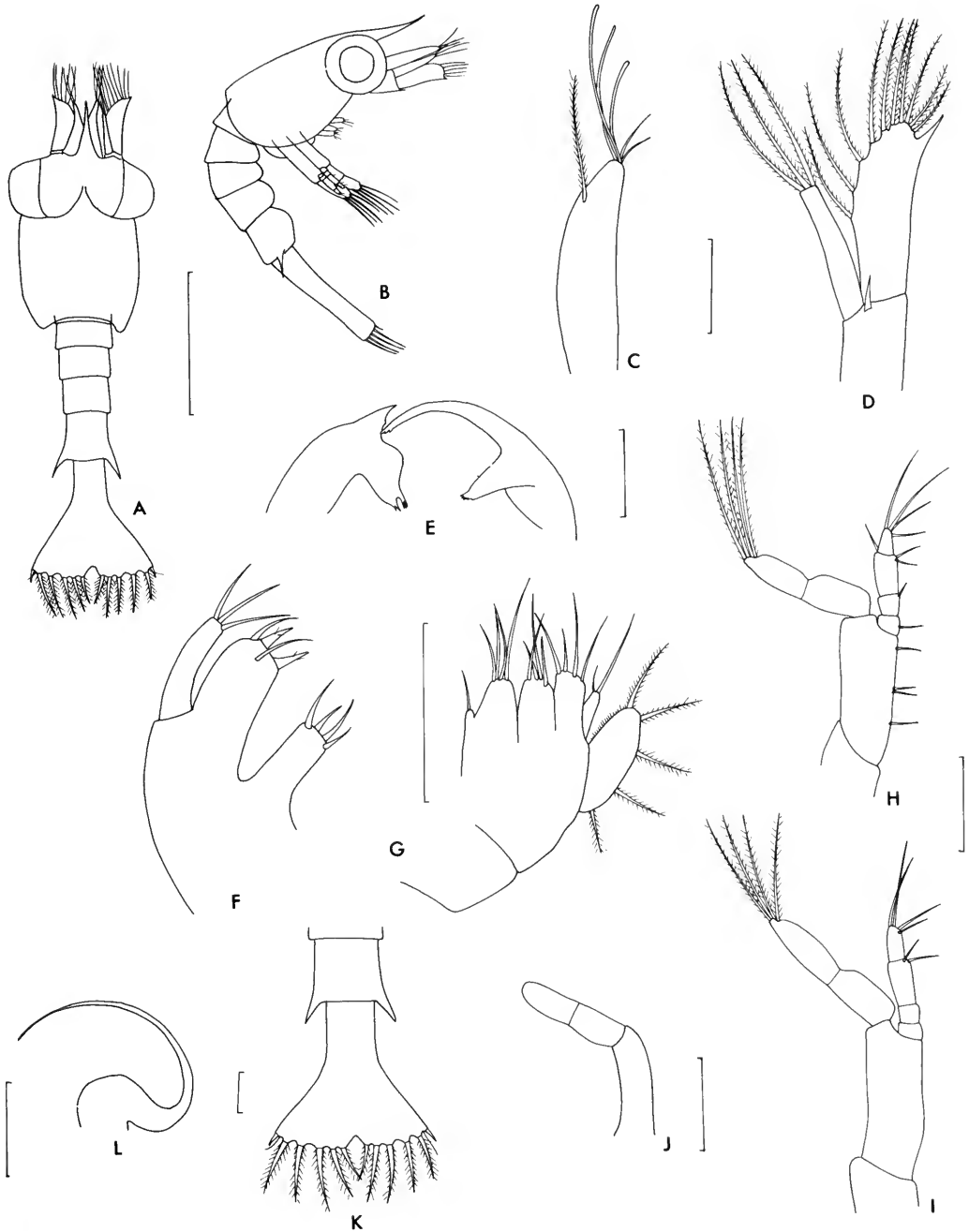
Fig. 13 *Axianassa* sp. Zoea I. A, dorsal view; B, lateral view; C, antennule; D, antenna; E, mandibles; F, maxillule; G, maxilla; H, I, J, first, second and third maxillipeds respectively; K, fifth abdominal segment and telson in dorsal view; L, left lobe of paragnath. Scale. 0·5 mm: A, B; 0·1 mm: C–L.
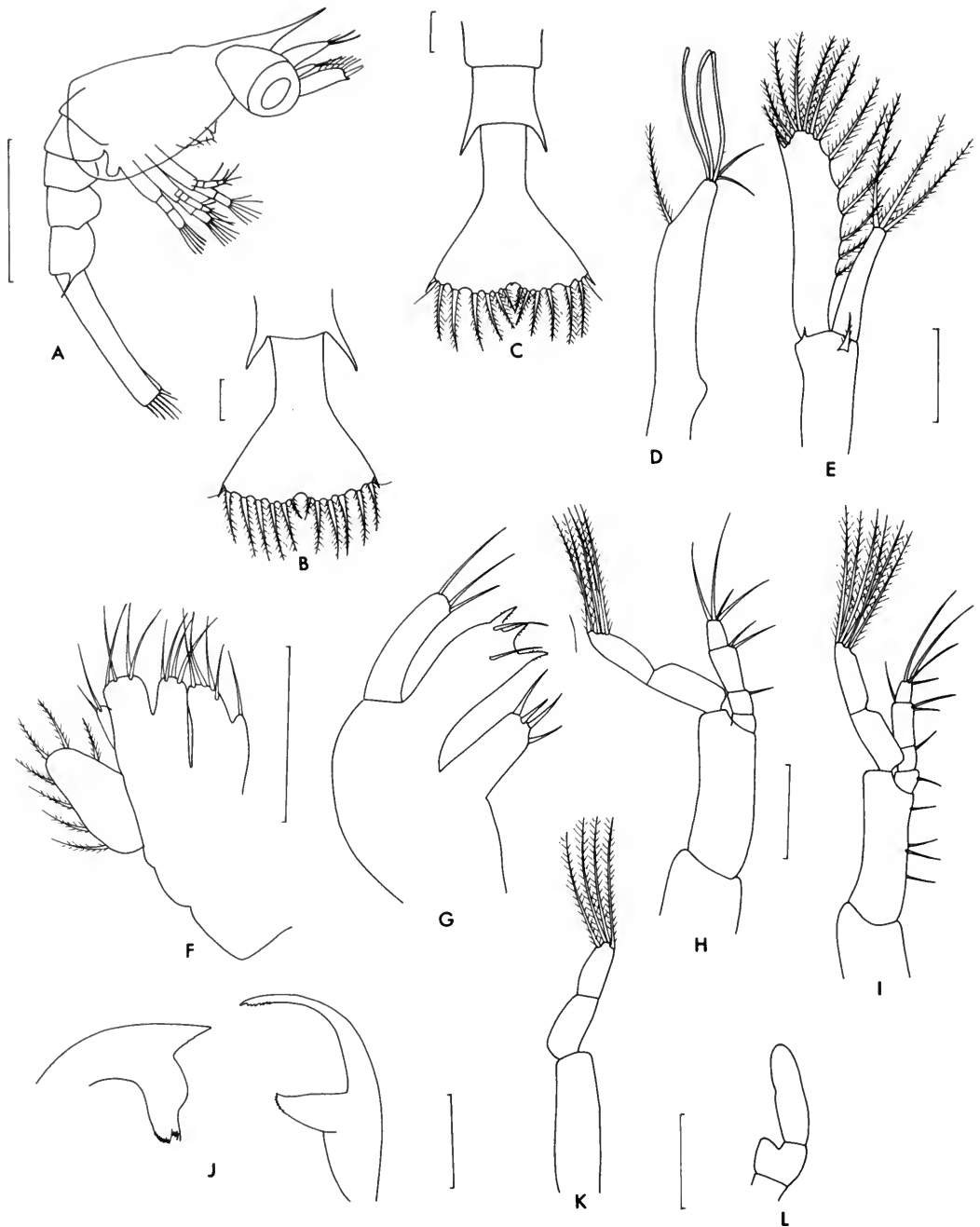
Fig. 14 *Axianassa* sp. Zoea II. A, lateral view; B, telson without median spine in dorsal view; C, telson with median spine in dorsal view; D, antennule; E, antenna; F, maxilla; G, maxillule; H, second maxilliped; I, first maxilliped; J, mandibles; K, third maxilliped; L, first pereiopod. Scale. 0·5 mm: A; 0·1 mm: B–L.
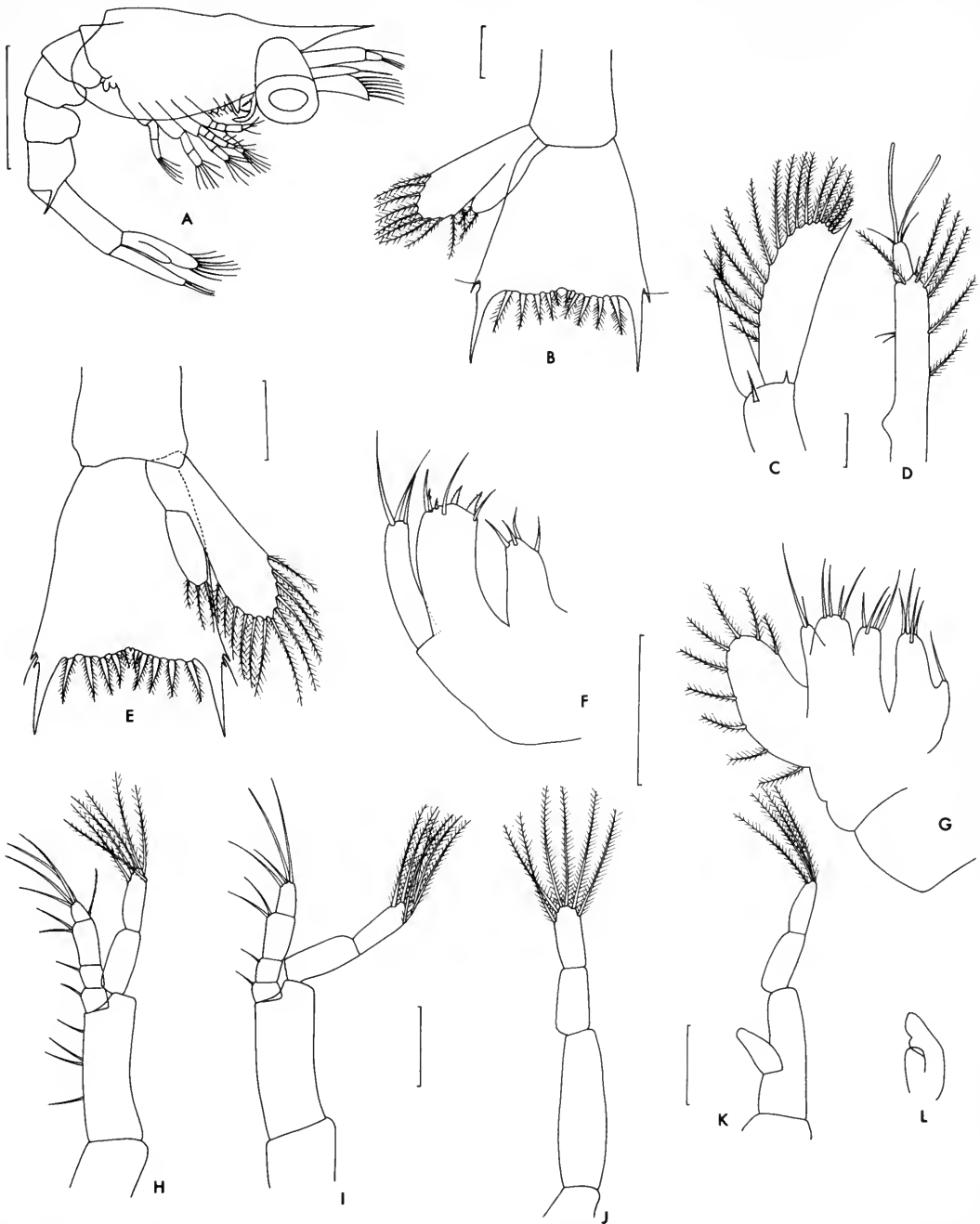
Fig. 15 *Axianassa* sp. Zoea III. A, lateral view; B, telson and uropods of form B in dorsal view; C, antenna; D, antennule; E, telson and uropods of form A in dorsal view; F, maxillule; G, maxilla; H, I, J, first, second and third maxillipeds respectively; K, L, first and second pereiopods. Scale. 0·5 mm: A; 0·1 mm: B–L.
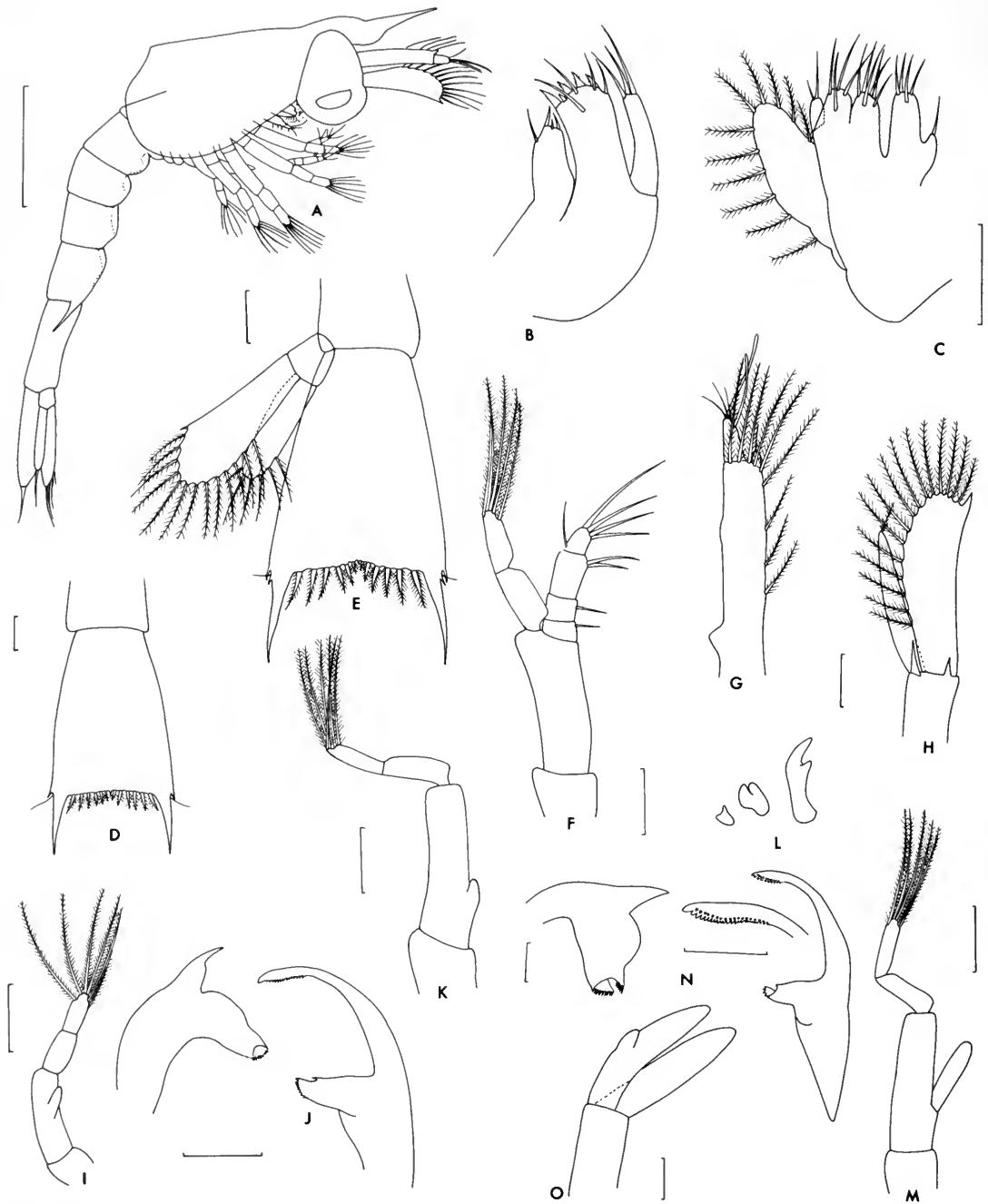
Fig. 16 *Axianassa* sp. Zoea IV (A–M) and last zoea (N, O). A, zoea IV in lateral view; B, maxillule; C, maxilla; D, telson of form B; E, telson of form A and uropods; F, second maxilliped; G, antennule; H, antenna; I, second pereiopod; J, mandibles; K, third maxilliped; L, from right to left, third, fourth and fifth pereiopods; M, first pereiopod; N, O, last zoea, mandibles and second pleopod. Scale. 0·5 mm: A; 0·1 mm: B–O.

Fig. 17 *Axianassa* sp. Last zoea. A, dorsal view; B, lateral view; C, antenna; D, antennule; E, F, G, first, second and third maxillipeds respectively; H, maxilla; I, maxillule; J, second pereiopod; K, first pereiopod; L, fourth pereiopod; M, third pereiopod; N, fifth pereiopod; O, telson and uropods in dorsal view. Scale. 1 mm: A and B; 0·1 mm: C–O.

The status of *Glyphocrangon rimapes* Bate, 1888 (Crustacea, Decapoda, Glyphocrangonidae)

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Introduction

In an excellent review of the genus *Glyphocrangon* in the Atlantic, Holthuis (1971) included *Glyphocrangon rimapes* Bate for the sake of completeness, although he had himself seen no specimens and, indeed, the species had not been recorded since Bate's (1888) original description based on material collected during the *Challenger* Expedition.

During an examination of decapods in the *Discovery* collections obtained in the north-eastern Atlantic in recent years, a number of specimens were identified with some difficulty as *rimapes* using Holthuis' key and prompted a re-examination of Bate's specimens since, as Holthuis pointed out, it was possible that these represented more than one species. In the event, the situation turned out to be rather more complicated than Holthuis imagined and, because of inadequacies in the original description, some minor changes are necessary to his key for the identification of the Atlantic species of the genus.

Bate (1888, pages 523–525) had before him four female specimens, one from Japan (stat. 237), two from near Juan Fernandez (stat. 300) and one from the South Atlantic near Tristan da Cunha (stat. 331). The illustration and the bulk of his description was based on the larger specimen from station 300, but Bate designated as the type the South Atlantic specimen. In Bate's list of material examined this latter specimen is described as an ovigerous female 87 mm in length,* and the specimen in the collection carrying the station 331 label agrees with this. Unfortunately, at the end of his description, and after dealing with the two specimens from station 300 near Juan Fernandez, Bate rather confuses the situation with the following statement.

> In the middle of the South Atlantic, at Station 331, another specimen was trawled which was nearly 87 mm long, and has no teeth on the bosses of the coxal plates of the pleon. Another specimen about the same length was trawled at Station 237, in which teeth on the lateral bosses of the pleon are present. This animal is well developed, and is a female laden with about thirty large ova.

However, the specimen labelled as coming from station 237 is a good deal smaller than that labelled as from station 331 and is not bearing eggs. It is almost certain that Bate's statement quoted above is simply a mistake and that the South Atlantic specimen, and therefore the holotype of the species, is indeed the ovigerous female labelled as such in the collection. In the absence of any further documentary evidence in the British Museum (Natural History), either to substantiate or to counter this conclusion, I am assuming that it is correct.

In the section on the genus *Glyphocrangon,* Bate deals with seven species. He gives an extensive generic diagnosis and a very long description of *Glyphocrangon granulosis,* but the accounts of the other species are rather short. In the case of *G. rimapes* the description is basically a comparison with *G. granulosis* from which Bate distinguished it mainly on (1) having three pairs of teeth on the rostrum instead of two, (2) having a more prominent mid-dorsal crest running from the rostrum onto the carapace, (3) having rather longer spines on the pleural plates of the abdominal somites, (4) having teeth on the bosses on the lateral

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*Bate's total lengths apparently exclude the rostrum.

surfaces of some of these plates, and (5) having bifid tips to the dactyls of the last pair of legs. By implication, Bate's description therefore indicates that in other major features *G. rimapes* resembles *G. granulosis.* This would include the presence of only two spines on the pleuron of the fifth abdominal somite, as is the case in most species of the genus. Unfortunately, the illustration in the *Challenger Report,* reproduced by Holthuis, appears to confirm this situation and Holthuis accordingly used this character very early in his key to separate off *Glyphocrangon sculpta* (Smith), the only Atlantic species which he thought possessed three pleural spines on this somite. In fact, the possession of three spines on the fifth somite is one of the most characteristic features of *G. rimapes,* although the third spine is admittedly missing from one side of the holotype. *G. rimapes* therefore keys out in Holthuis's key together with *G. sculpta* from which it can be distinguished on the rostral armature.

In view of these problems, and the fact that *G. rimapes* appears to be the only species reported from both the Atlantic and the Pacific, a redescription of the species in the light of the additional Atlantic material available, together with a re-assessment of the status of the Pacific specimens, seems warranted.

Glyphocrangon rimapes Bate, 1888

Glyphocrangon rimapes Bate, 1888, *Rep. Voy. Challenger,* Zool. **24** : 523, pl. 94, fig. 4—Holthuis, 1971, *Bull. mar. Sci.* **21** : 287, fig. 4. (Holthuis gives an extensive series of references, but none of them deal with new specimens or even with a re-examination of the original material.)

DESCRIPTION. *Holotype:* Ovigerous female from *Challenger* Station 331 (March 9, 1876); 37°47'S: 30°20'W, 1715 fathoms (3138 m). C.L. (carapace length) 46·8 mm; T.L. (total length including the rostrum) c. 112 mm; P.O.C.L. (post-orbital carapace length) 27·4 mm (Figs 1A; 2A; 3A).

The carapace is glabrous. The rostrum extends just beyond the antennal peduncle and for about 1/4 of its length beyond the scaphocerite, this section being fairly strongly upturned. The dorsal surface of the rostrum is more or less flat distally, becoming slightly concave proximally; throughout its length it has a slight median ridge which breaks up into a series of seven or eight small spines behind the level of the eyes, increasing in size posteriorly and ending between the posterior lateral rostral spines. The dorso-lateral margins of the rostrum carry four spines on either side, a large one anterior to the eyes, two smaller ones close together immediately behind the eyes, and a very small spine immediately behind these. From this point the continuations of the rostral margins diverge strongly to end in a broad-based spine on either side at the anterior end of the anterior intermediate carina.

The antennal spine is directed strongly forwards and upwards, but only slightly outwards. The branchiostegal spine is directed strongly forwards, but is more or less horizontal so that it is parallel with the rostrum in lateral view. In dorsal view it is also more or less parallel with the antennal spine.

The anterior submedian carinae each carry about eight spiniform tubercles with scattered rather blunt tubercles between the two carinae medially. Laterally there are more blunt tubercles arranged in two rather indefinite and irregular rows, one close to the anterior submedian carinae, and one close to the anterior intermediate carinae. The latter are not well-defined, but consist of four spiniform tubercles and the strong anterior spine at the end of the continuations of the rostral margin.

The posterior submedian and intermediate carinae are not very clear, but are each marked by about four somewhat larger and more spiniform tubercles than those scattered between them.

The anterior antennal carina is not apparent; the region where it should run, between the anterior lateral carina and the lateral groove, simply carries a series of about 16 blunt tubercles. The posterior antennal carina, however, is a well-marked ridge running from the lateral groove to the postero-marginal groove and incorporating a series of tubercles which increase in size slightly posteriorly. Again there are scattered tubercles between the posterior
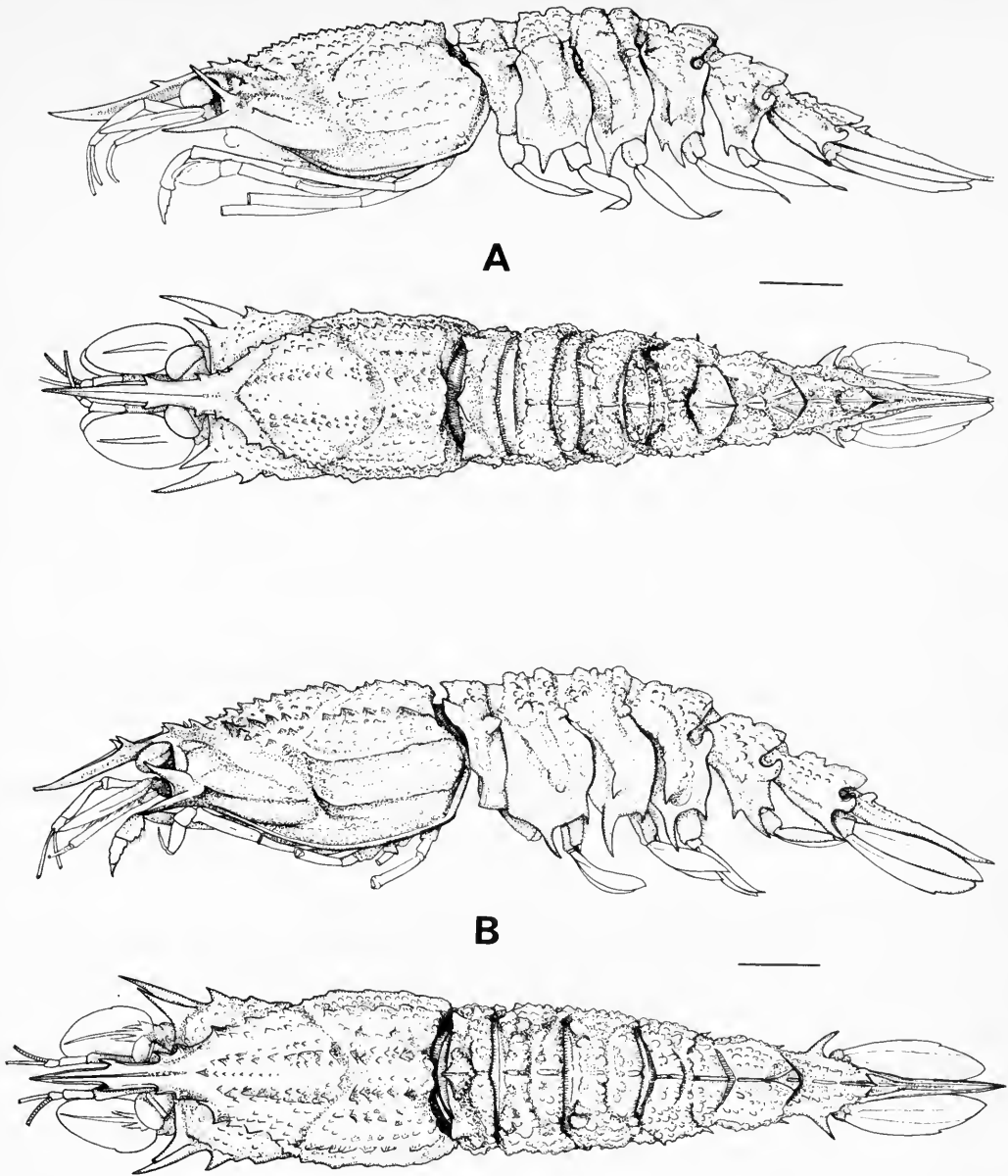
Fig. 1 *Glyphocrangon rimapes* Bate, 1888. A, holotype female from H.M.S. *Challenger* station 331. B, paratype female (C.L. 49·6 mm) from H.M.S. *Challenger* station 300. The bar scales represent 10·0 mm.

antennal carina and the posterior submedian carina, roughly arranged in three longitudinal rows.

The anterior lateral carina is quite well-marked and begins at a strong tooth at the base of the branchiostegal spine. Posteriorly the carina consists of a raised reticulated ridge of the integument running to the lateral groove. Beyond the groove the posterior lateral carina continues as a quite sharp, but not greatly raised ridge.

The anterior sub-lateral and sub-marginal carinae seem to be represented by two rather ill-defined reticulated areas of the integument, but separated by a very distinct groove

running from the end of the lateral groove towards the antero-lateral carapace margin. Unfortunately, the carapace is damaged on both sides in this region, (possibly by Bate in examining the branchiae which are rather disturbed), but the two carinae seem to be continued beyond the lateral groove as reticulated lines ending close to the postero-lateral carapace angle inside which there is a fairly strong tubercle.

The tubercles on the abdomen are generally rather blunt and crowded. The three large spines on the first somite are triangular and sharp and the mid-dorsal spine is followed by a small spine which is really the posterior section of the median carina. The median carina is interrupted in the middle on somites two and three, and rather more anteriorly on somites 4–6. On the fifth somite the sub-median carinae are well-marked, running from the end of the anterior median carina to the end of the somite. On the sixth somite the anterior component of the median carina is armed with two teeth and the posterior component ends in an acute point. The ventral margin of the pleuron of the second somite has a long spine medially, the postero-lateral angle carries a small spine, while the antero-lateral angle is more or less rectangular but unarmed. The boss in the centre of this pleuron carries a number of tubercles but these are not developed into spines. The pleuron of the third somite is armed with two teeth, the anterior being about three times as long as the posterior and more or less continuous with the anterior margin of the pleuron. The pleuron of the fourth somite is armed with three spines, the median the largest and the anterior the smallest. The bosses on the third and fourth somites are both armed with strong, downwardly directed conical spines. The pleuron of the fifth somite on the right hand side is armed with three spines, the median the longest and the posterior the smallest. This posterior spine is absent on the left hand side. The pleuron of the sixth somite ends in a strong backwardly directed spine which over-reaches the protopodite of the uropods.

The dorsal surface of the telson carries a large and a small conical spine anteriorly in the mid-line, and the sub-median carinae carry about 18 serrations which become smaller and more widely spaced posteriorly. The tip of the telson is broken, but it appears to over-reach slightly the blades of the uropods.

The antennal peduncle over-reaches the scaphocerite by the length of the distal segment. The outer margin of the scaphocerite carries no teeth.

The endopodite of the third maxilliped does not quite reach to the end of the scaphocerite.

The propodus of the first pereiopod reaches about half-way along the first segment of the antennular peduncle.

The second pereiopods are sub-equal, but the carpus of the left one consists of 17 segments and that of the right about 20.

The third pereiopod over-reaches the scaphocerite by the length of the dactyl, which is about 1/3 the length of the propodus and is slender and styliform.

The fourth pereiopod over-reaches the scaphocerite by the length of the dactyl, while the last pereiopod reaches just to the end of the scaphocerite. The dactyls of both the fourth and fifth pereiopods are somewhat flattened, widest in the middle, grooved on their outer surfaces and have bifid tips. Their bases are each surrounded by a fringe of hairs on the end of the propodus.

The ova, of which there are about 35, are approximately 3·0 mm in diameter.

The remaining syntype material. 1. Non-ovigerous female from *Challenger* station 300 (December 17, 1875), 33°42′S; 78°18′W, 1375 fathoms (2516 m), C.L. 49·6 mm, T.L. c. 123 mm; P.O.C.L. 31·4 mm (Figs 1B; 2B; 3B).

This is the largest of the two specimens from this station and is the one on which Bate's description and illustration was apparently based. It is very similar to the holotype, differing from it only in the following details.

The rostrum is rather shorter, not reaching quite to the end of antennal peduncle and only just over-reaching the scaphocerite. The dorsal surface of the rostrum is concave throughout its length and has a more prominent median ridge than in the holotype. The dorso-lateral rostral margins carry three pairs of spines which are rather more prominent than those in the
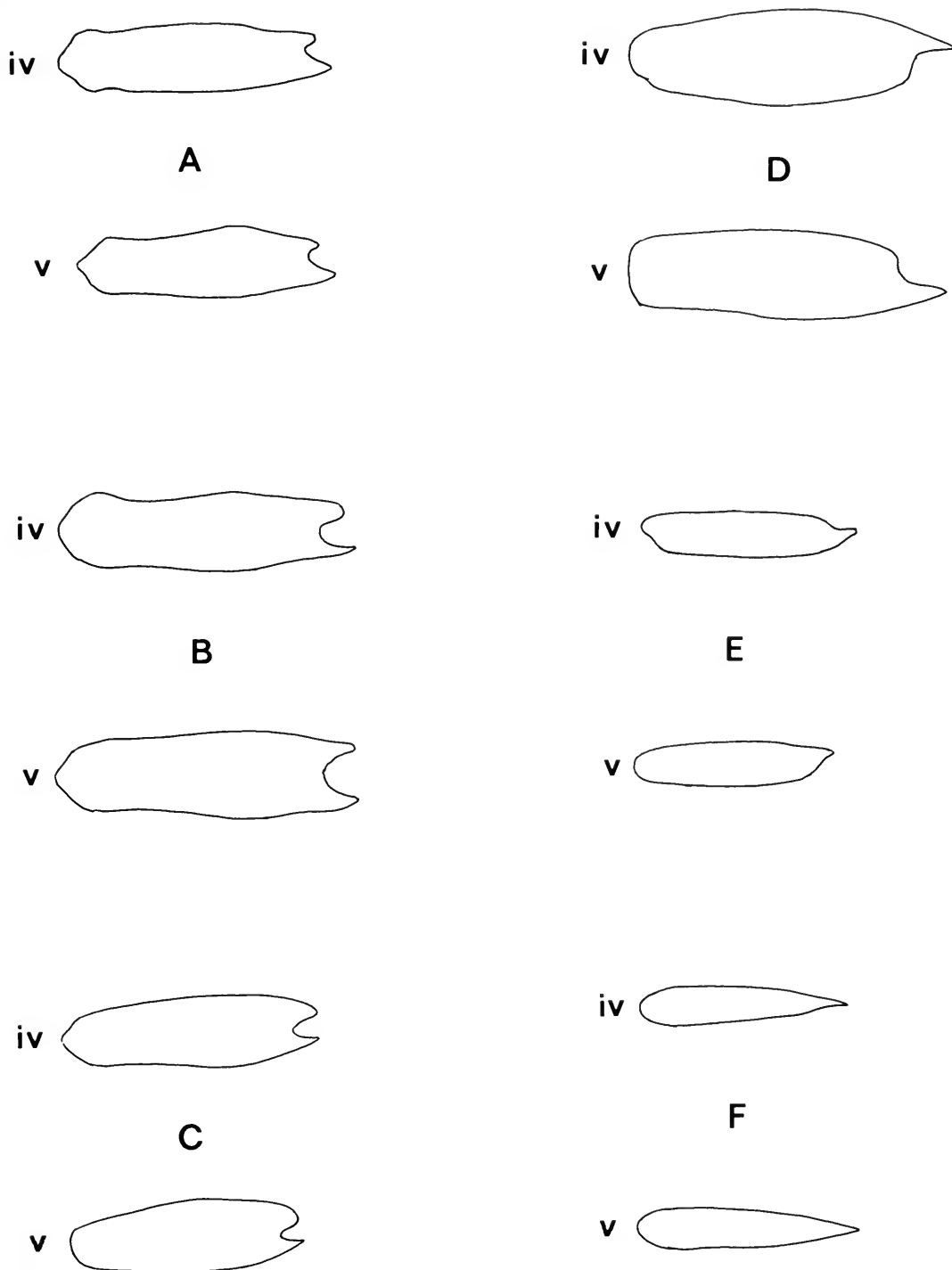
Fig. 2 *Glyphocrangon rimapes* Bate, 1888. Dactyls of the fourth (IV) and fifth (V) pereiopods. A, holotype female; B, paratype female (C.L. 49·6 mm) from H.M.S. *Challenger* station 300; C, ovigerous female (C.L. 44·8) from *Discovery* station 9640; D, paratype female (C.L. 33·2 mm) from H.M.S. *Challenger* station 300; E, male from *Discovery* station 9640; F, male from R.V. *Challenger* station 50604. Not all drawn to same scale.

holotype, but the small fourth pair are missing. The antennal spines are more obliquely directed than in the holotype so that in dorsal view they converge upon the branchiostegal spines rather than running parallel to them. The remainder of the carapace is very similar to that of the holotype except that the tubercles are generally a little more prominent, those at the end of the posterior median carinae overhang the posterior marginal groove as a bifid projection, and the anterior lateral carinae carry two fairly well-marked teeth on the right hand side and one tooth on the left, in addition to the strong anterior one.

On the abdominal somites the ventral spines on the pleural plates are generally rather longer than those of the holotype, but there are only two spines on the pleura of the fourth somite and three on both sides of somite five. The spines on the lateral bosses on somites three and four are better developed and more acute than in the holotype.

The scaphocerite has no properly developed outer tooth, but there is a slight protruberance on the outer margin.

The third maxilliped is slightly longer than in the holotype and reaches the end of the scaphocerite.

The carpus of the second pereiopod consists of only 18 segments on the right hand side and 15 on the left.

The third pereiopods are missing, but the dactyls of the fourth and fifth pereiopods are bifid, as in the holotype. However, in this specimen the dactyls each have a boss close to the articulation with the propodus which prevents the dactyl being flexed beyond about 90° with the propodus.

2. Non-ovigerous female from *Challenger* station 237 (June 17, 1874), 34°37′N; 140°32′E, 1875 fathoms (3431 m), C.L. 38·0 mm; T.L. c. 90·0 mm, but telson tip broken; P.O.C.L. 24·0 mm (Fig. 3D).

This specimen closely resembles the holotype, and particularly the large specimen from Juan Fernandez, different only in the following.

The lateral rostral margin carries three teeth on the left hand side and four on the right, the extra one being a small tooth between the posterior pair, not represented in either of the other two specimens. The anterior lateral carinae each have a prominent posterior tooth and, between this and the anterior tooth, a single very small tooth on the right hand side and two on the left.

The abdomen is very similar to that of the Juan Fernandez specimen except that the antero-ventral corners of the pleura of the first somite are produced forwards as short, blunt spines, the spines on the bosses of somites three and four are less acute, and the ventral teeth on the pleura are shorter and more like those of the holotype, while the pleuron on the left hand side of somite five carries three teeth.

The appendages are very similar to those of the holotype, the scaphocerite having almost no suggestion of a marginal spine, the carpus of the second pereiopod consisting of 21 segments on the right hand side and 18 on the left, and the bifid dactyls of pereiopods four and five lacking the basal bosses present on the Juan Fernandez specimen.

3. Non-ovigerous female from *Challenger* station 300 (see specimen 1, above), C.L. 33·2 mm; T.L. c. 77·2 mm; P.O.C.L. 18·0 mm (Figs 2D & 3C).

Apart from being considerably smaller, this specimen differs from the others of the type series in a number of features.

The rostrum is considerably longer, over-reaching the antennal peduncle by about one quarter of its own length and the stylocerite by about one third; it broadens significantly in its distal half and the dorsal surface has distinct corrugations. The dorso-lateral margins carry three pairs of spines, but the posterior pair are very small. The carinae and grooves of the carapace are much the same as in the other specimens, but the tubercles are generally much less well-defined and tooth-like. The anterior tooth on the anterior lateral carina is broad-based and not very acutely tipped, while the single tooth behind this is also very broad based and poorly defined.

The dorsal and lateral surfaces of the abdomen are also generally like the other type specimens, but, as on the carapace, the tubercles are less numerous and less tooth-like. The
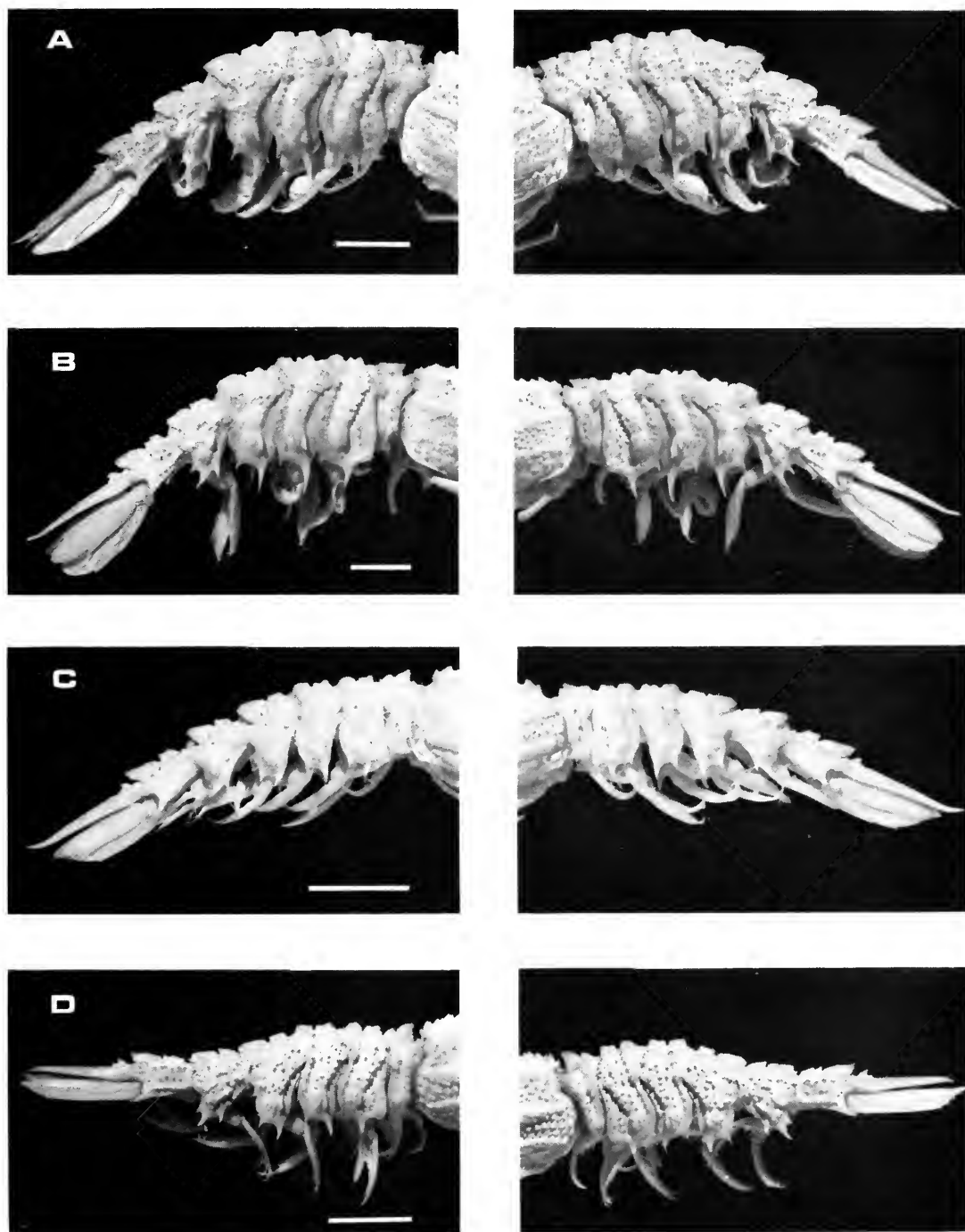
Fig. 3 *Glyphocrangon rimapes* Bate, 1888. Right hand side and left hand side views of the abdomens of the type series to show variations in the pleural spines. A, holotype; B, paratype (C.L. 49·6 mm), H.M.S. *Challenger* station 300; C, paratype (C.L. 33·2 mm), H.M.S. *Challenger* station 300; D, paratype, H.M.S. *Challenger* station 237. The bar scales represent 10·0 mm.

Table 1 Material of *Glyphocrangon rimapes* Bate examined

Station	Position	Depth (m)	Sex	C.L.(mm) (A)	P.O.C.L.(mm) (B)	T.L.(mm)	A/B	Remarks	B.M.(N.H.) reg. no.
HMS *Challenger* 331	37°47·0'S: 30°20·0'W	3138	♀	46·8	27·4	c 112·0	1·71	Holotype (ovig.)	88:33
HMS *Challenger* 300	33°42·0'S: 78°18·0'W	2516	♀	49·6	31·4	c 123·0	1·58	Paratype	88:33
			♀	33·2	18·0	c 77·2	1·84	Paratype	88:33
HMS *Challenger* 237	34°37·0'N: 140°32·0'E	3431	♂	38·0	24·0	c 90·0	1·58	Paratype	88:33
RRS *Discovery* 9638	49°50·2'N: 147·3'W	4043–4104	♀	35·3	20·6	c 87·0	1·71		1980:188
RRS *Discovery* 9640	50°3·2'N: 13°50·6'W	3749–3757	♀	44·8	26·7	c 109·2	1·68	ovig.	1980:189
			♀	37·3	21·3	?	1·75		1980:190
			♂	39·2	22·4	c 96·0	1·75		1980:191
RV *Challenger* 50512	50°13·6'N: 13°34·5'W	3022–3110	♀	41·4	24·8	c 100·7	1·66	ovig.	1980:192
			♀	45·4	25·5	c 104·5	1·80	ovig.	1980:193
RV *Challenger* 50604	50°6·1'N: 13°53·0'W	3490–3550	♂	22·3	11·7	c 51·5	1·90		1980:194

bosses on the pleura of somites three and four are quite pronounced but, as Bate pointed out, they are not armed with teeth. The pleura of somites 2–5 each carry only two ventro-lateral spines.

The outer margin of the scaphocerite has a small notch, as in the other Pacific specimens, but this seems to be more distally placed. Several of the more posterior appendages are damaged but the second pereiopods have the carpus divided into about 20 segments on the right hand side and about 15 on the left. Finally, the dactyls of pereiopods four and five are not bifid, but have a stepped outline and terminate in a single acute tip; they do not have a basal boss.

NEW MATERIAL. During a series of cruises undertaken since 1977 to investigate the benthic fauna of the Porcupine Sea-Bight to the south-west of Ireland, a further four female and three male specimens of *G. rimapes* have been collected at depths ranging from about 3000 m to a little over 4000 m (see Table 1).

The females all resemble the holotype but are even more similar to the large specimen from station 300 since, like it, they have only three pairs of spines of the rostral margin, the pleura of somite four carry only two spines, while there are consistently three spines on the pleura on each side of somite five. The only significant difference between these specimens and those of the type series is that the spines on the bosses of the pleura of somites three and four are rather less well-developed.

The two largest male specimens resemble the recently collected females very closely, although the pleural spines are rather shorter and there is a suggestion of a third spine on the fourth abdominal somite (see Fig. 4C). The main distinction from the females, however, is that while the dactyls of the fourth and fifth pereiopods are more flattened than those of the styliform third pair, they end in a single point and at most have a step near the tip (see Fig. 2E). Thus, as in *Glyphocrangon sculpta* (see Holthuis, 1971; Barnard, 1950) it is only the females which have the characteristic bifid dactyls.

The smallest male (from station 50604) has a well-developed appendix masculina and non-bifid dactyls on the last two pereiopods. However, it differs from the other males, and from most of the females, in having a relatively much longer rostrum which over-reaches the scaphocerite by almost half its own length, in having the posterior rostral spines very much smaller than the more anterior ones, and in having a quite prominent notch in the outer margin of the scaphocerite slightly anterior to its mid-point.

DISCUSSION. The suggestion by Holthuis (1971, p. 287) that Bate's specimens might include more than one species was presumably prompted by the wide separation of the localities from which they were obtained, together with the fact that no other species of the genus had been recorded from both the Atlantic and from the Indo-Pacific. From an examination of the type series alone, I would have had little hesitation in concluding that three of the four specimens, that is the holotype from the southern Atlantic, the specimen from off Japan and the larger of the two specimens from Juan Fernandez, belong to the same species despite the slight differences, particularly in the pleural armature, between them. The fourth specimen, that is the smaller female from Juan Fernandez, is rather different since, not only does it have a distinct pleural armature with only two spines on the fifth somite, but it lacks the bifid dactyls on the fourth and fifth pereiopods, it has a very reduced posterior rostral spine, and a relatively longer rostrum. With the additional north-Atlantic material available, however, these variations seem to be acceptable. For although the pleura of the fourth and fifth abdominal somites usually have two and three teeth respectively, these are quite variable. Similarly, while the rostrum always apparently has at least three pairs of lateral spines, the posterior pair may be very small, particularly in juvenile specimens, while additional spines may be present. Finally, the rostrum becomes relatively shorter in older specimens, being almost twice the post-orbital carapace length in the smallest specimen available and less than two thirds as long in the largest.

The new material extends the known depth range of *G. rimapes* from 2500 m to 4100 m
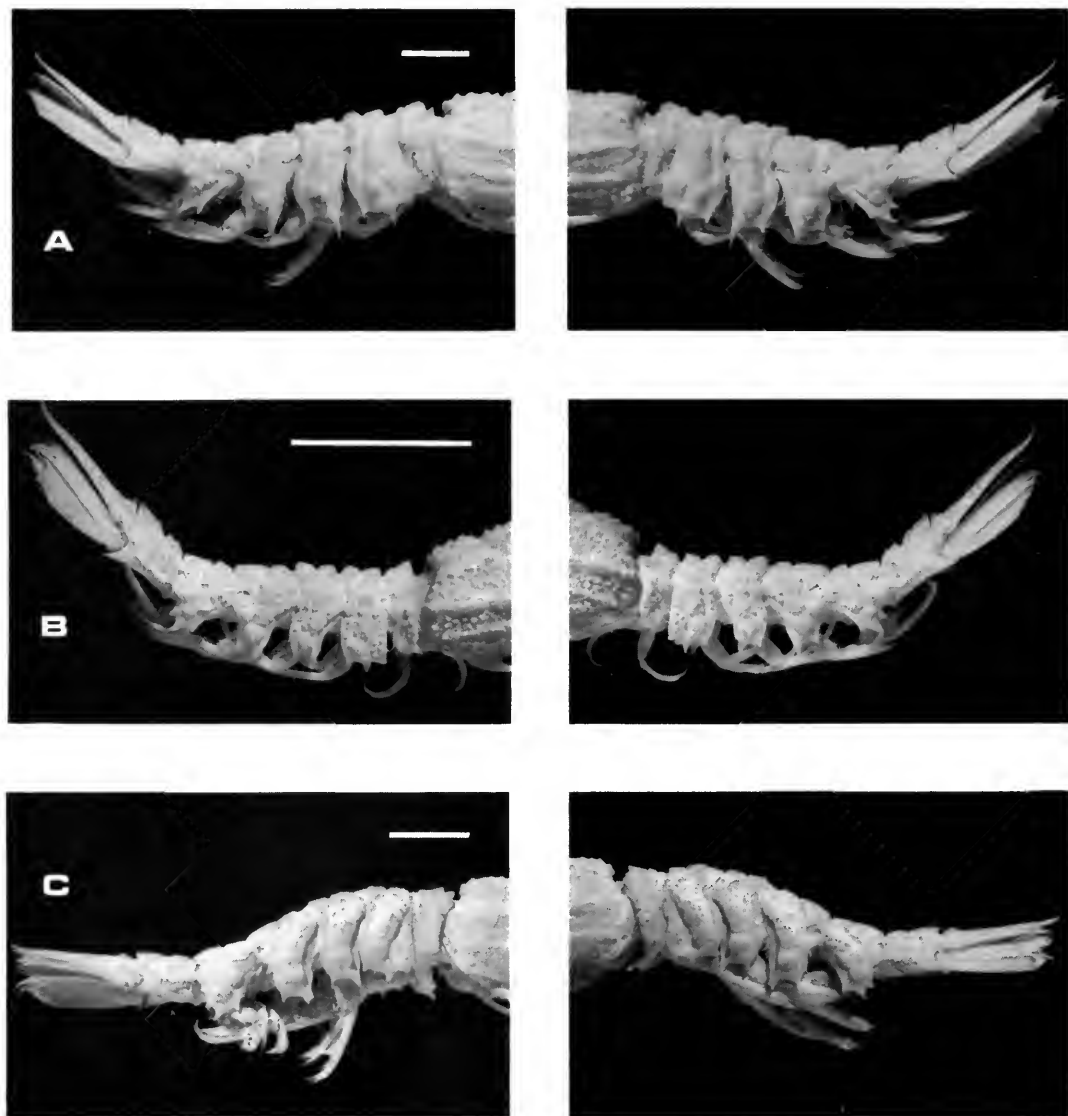
Fig. 4 *Glyphocrangon rimapes* Bate, 1888. Right hand side and left hand side views of the abdomens of three specimens from the Porcupine Sea-Bight. A, female (C.L. 44·8 mm), *Discovery* station 9640; B, male, R.V. *Challenger* station 50604; C, male, *Discovery* station 9640. The bar scales represent 10·0 mm.

and the horizontal distribution to include the northeastern Atlantic. In the Porcupine Sea-Bight region *rimapes* overlaps at the shallower end of its range with *G. sculpta* (Smith) and is replaced at depths a little over 4000 m by *G. atlantica* Chace.

In order that Holthuis's key should cope adequately with *rimapes,* his third couplet should be removed and *rimapes* should be distinguished from all other Atlantic species at the beginning of the key by the presence of at least three pairs of rostral spines in this species.

Acknowledgements

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examine the type material from the *Challenger* collections. My thanks are also due to Mrs C. E. Darter for making the illustrations and to Mr A. F. Gray for photographing the specimens. Finally, I must thank Jonathan Rees for recognizing the *rimapes* problem in the first place.

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Crab zoeae and brachyuran classification: a re-appraisal

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Introduction

In a recent paper (Rice, 1980*a*) I reviewed the available information on crab zoeal morphology and attempted to assess its bearing on the classification of the Brachyura. Although zoeal evidence had already been employed several times to try to elucidate specific problems of crab relationships, there had been no previous attempt to relate a general classification based on the larval stages to that based on the adults. The reasoning behind the study was founded on the hope that since the zoeal stages are all adapted for a mid-water existence any classification based on them would be largely free from the problems associated with the convergent and divergent adaptations of the adults to their varied life styles. Using a variety of zoeal features, including details of the appendage setation, I was able to demonstrate, at least to my own satisfaction, a high degree of agreement with the traditional adult classification at the family level, but much less congruence at higher levels. For example, the zoeal stages of the constituent families of the Oxystomata are so distinct from one another that they confirm the doubts about the validity of this grouping which have been expressed by several students of adult crabs. Not only are there no zoeal grounds for grouping the dorippids, leucosiids and calappids together, but there is no support for their separation, either collectively or individually, from the Brachyrhyncha. Similarly, the clear differences between the zoeae of the parthenopids, hymenosomatids and majids argue strongly against their inclusion in a separate oxyrhynchous group, for the former two families, like the oxystomes, clearly seem to belong to the Brachyrhyncha. The majids, on the other hand, did seem to warrant separation from the majority of crabs, for their zoeae exhibit a number of distinctive features which indicate an early divergence and the adoption of a different developmental strategy from that of the rest of the Brachyura.

In dividing up the Brachyrhyncha the zoeal stages seemed to be much less helpful. Only two major groups were recognized; first a collection of families with relatively primitive larvae corresponding roughly with Milne Edwards' Cyclometopa or Guinot's (1978) Heterotremata, and a second group with more advanced larvae which corresponds fairly closely with Milne Edwards' Catometopa or Guinot's Thoracotremata. Such a division, however, seemed to be very artificial since it grouped the families according to their general evolutionary level rather than into phylogenetic lineages. Moreover, there were some important discrepancies between the larval divisions and those suggested by Guinot based on the morphology of the sexual organs in the adults. In particular, the Leucosiidae, which Guinot placed in her Heterotremata because at least some members of this family have coxal male sexual openings, have very advanced zoeal stages which seemed to ally them to the catometopous families which Guinot placed in her Thoracotremata.

During recent months the debate on brachyuran relationships has progressed somewhat, for in two most interesting notes Saint-Laurent (1980*a* & *b*) has generally supported Guinot's division of the Brachyura into the Podotremata, Heterotremata and Thoracotremata, but has disagreed fundamentally in her interpretation of the relationships between them.

The main diagnostic differences between Guinot's suggested groups are the positions of the male and female sexual openings: in the Podotremata both the male and female openings are coxal; in the Heterotremata the female openings are all sternal, but at least some species in

each family have the male openings on the coxa; in the Thoracotremata both the male and female openings are consistently sternal. Guinot suggested that during brachyuran evolution there has been a strong tendency for the sexual openings to move from the primitive decapodan coxal position onto the sternum and that her three sections therefore represent successive stages in this migration.

Saint-Laurent, on the other hand, sees great difficulty in deriving these groups from one another. She points out (1980a, p. 1266) that the female genital apparatus in the Podotremata is comparable with that in many other decapodan groups in which the spermatophores are deposited with the aid of the male sexual pleopods into a receptacle, the thelycum, formed from an intersegmentary fold of the integument and without any connection with the oviducts. Fertilization in these forms is external and takes place after egg-laying. Within the Sternitremen crabs (that is the Heterotremata and Thoracotremata together, or the Eubrachyura in Saint-Laurent's terminology) the spermatic mass is deposited, again via the sexual pleopods, in an internal seminal chamber formed by a dilation of the oviduct, within which fertilization takes place. Saint-Laurent finds it difficult to envisage the intermediate stages between one situation and the other involving, as it would, not only the loss of the thelycum but also a change in the orientation of the male sexual pleopods from the thelycum towards the oviducts. Instead, she suggests that the separation between the Podotremata, on the one hand, and the Heterotremata and Thoracotremata, on the other, is cladistic and not simply a difference of evolutionary level. Whether the Eubrachyura were derived from ancestors with or without a thelycum, Saint-Laurent concludes that they represent an independent branch which became separated at an early stage from the primitive brachyuran line.

Similarly, Saint-Laurent believes that the distinction between the coxal and sternal position of the male orifice is a fundamental one, indicating that the Heterotremata and Thoracotremata diverged at a very early stage in brachyuran evolution (see Fig. 1). She redefines the Heterotremata as eubrachyurans in which the male genital ducts always pass via the coxae of the fifth legs before opening to the exterior, either on the coxa itself or on the sternum. In the Thoracotremata the ducts always open to the exterior directly through the sternum without passing via the coxae. Guinot had suggested that some heterotrematous groups, such as the Goneplacidae and Leucosiidae, in which the male orifices are, in her terms, sometimes coxo-sternal, represent an intermediate stage towards the thoracotrematous condition. Saint-Laurent, on the other hand, sees these groups as being truly heterotrematous since the male orifice only *appears* to be sternal because the tubular prolongation of the male duct, that is the penis, becomes encapsulated after it leaves the coxa within an integumentary canal at the boundary between sternites seven and eight, to emerge finally in a sternal position. The tendency of the male orifices to move towards the mid-line in both the Heterotremata and the Thoracotremata is seen by Saint-Laurent as a response to the relative narrowing of the anterior abdominal somites compared with the posterior cephalothorax, and the need to bring the orifices close to the bases of the sexual pleopods to ensure successful sperm transer. But she considers the mechanisms by which this has been achieved in the two groups as totally distinct.

Consequently, Saint-Laurent's view of brachyuran phylogeny (see Fig. 1) is rather different from that put forward by most authors in the past and implied by Guinot. For while most authors have derived the higher Brachyura from within the Podotremata, Saint-Laurent does not identify ancestors for either the podotrematous groups or the Eubrachyura, but she suggests that they diverged at a very early stage. Similarly, although she indicates that the Heterotremata and the Thoracotremata had a common ancestor, she maintains that the Heterotremata diverged very early on, possibly via more than one line, and that the ancestors of the Thoracotremata are not to be found amongst the extant Heterotremata or their immediate predecessors. Finally, she suggests that the assumption of the thoracotrematous condition, in which the posterior thoracic appendages are freed from any involvement in reproduction, may have allowed the development of highly perfected locomotory mechanisms and enabled this group to colonize a variety of terrestrial habitats.
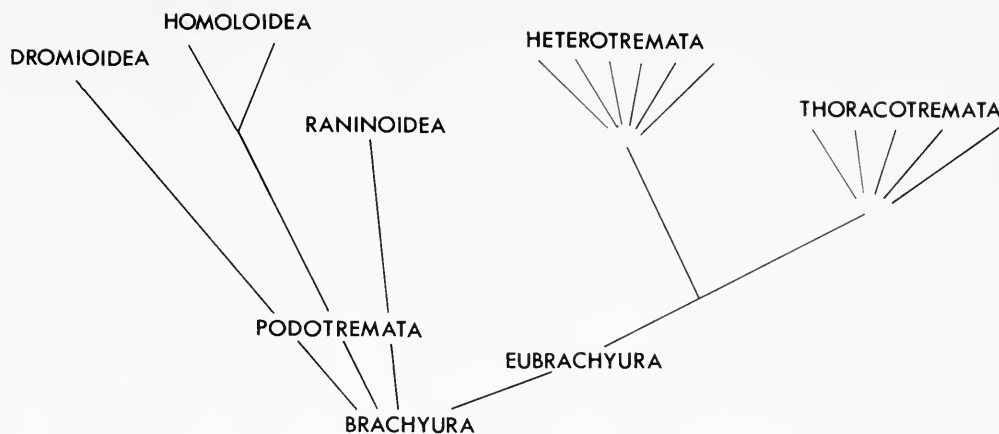
Fig. 1 Summary of the phylogenetic relationships of the main brachyuran groups according to
Saint-Laurent (modified from Saint-Laurent 1980*b*).

The publication of this new approach to brachyuran phylogenetics has prompted me to
re-examine the zoeal evidence for crab inter-relationships and, in a later publication, to
consider also the megalopa stage.

PODOTREMATA

Guinot's Podotremata contains the dromiids, homolids, raninids and tymolids, the last three
groups being placed together in the subsection Archaeobrachyura.

After discussing the zoeal evidence at some length (Rice, 1980*a*, p. 289 *et seq*.) I supported
Williamson's (1965, 1976) view that the Dromioidea are more closely related to some of the
anomuran groups than to the brachyurans and should accordingly not be included in the
latter. This conclusion was based on a number of generally anomuran features of dromioid
zoeae, but particularly on the presence of the hair-like second telson seta in all known
dromiid zoeae, and in the anomurans and thalassinids, but its absence from all higher
brachyurans. Knowledge of dromioid larvae was at that time limited to those of the
Dromiidae, and Williamson (1976, p. 407) had suggested that larvae of the families
Homolodromiidae and Dynomenidae might be much more homolid (that is brachyuran). No
homolodromiid larvae have yet been described, but an examination of the late embryos of
the dynomenid *Acanthodromia erinacea* H. Milne Edwards (Rice, in press) has demon-
strated that the zoea is very similar to known dromiids, including the presence of a
hair-like second seta. Thus, there is still no larval evidence of a more brachyuran branch of
the Dromioidea and I therefore remain convinced that they should not be included within
the Brachyura.

In establishing her Archaeobrachyura, Guinot (1978) recognized that it was not a natural
group since, she maintained (p. 232), 'ils comportent à la fois des espèces primitives, qui sont
sans doute à l'origine des autres sections (les "vrais Crabes"), et des espèces apomorphes avec
des caractéristiques spéciales aux trois super-familles.' From the zoeal evidence I also
concluded that this grouping is not natural in the strictly cladistic sense since I believed that
the raninids became separated from the primitive brachyuran line at a later stage than that
which gave rise to the ancestral lineage of the extant homolids. Thus, I suggested (Rice,
1980*a*, Fig. 9) that the raninids and the higher brachyurans share a more recent common
ancestor than either group does with the homolids. I nevertheless felt that the archae-
obrachyuran concept is a useful one since it indicates that although the higher crabs
originated from an ancestor within it, they have attained a significantly higher evolutionary
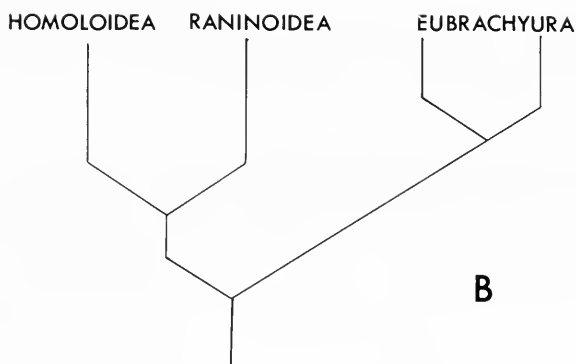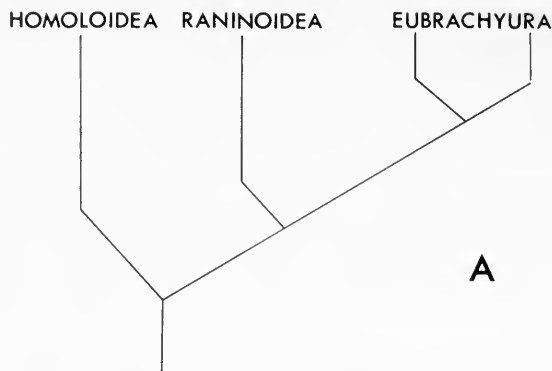
Fig. 2 Alternative phylograms showing the relationships of the homolids, raninids and eubrachyurans (see text).

level so that their separation from the raninids in terms of evolutionary change is much greater than that between the homolids and raninids.

Saint-Laurent did not give details of her opinion of the origin of the brachyuran groups. However, since she considers the divergence between the Podotremata and the Eubrachyura to be cladistic, she would presumably favour a phylogram for the homolids, raninids and eubrachyurans like Fig. 2B rather than 2A, that is with the homolids and raninids having a more recent common ancestor than the raninids and the eubrachyurans. It seems to me that the apomorphic characters shared by the zoeae of the raninids and the Eubrachyura, but not by the homolids, argue strongly against this and I would therefore still contend that the homolids became separated from the primitive brachyuran line at an earlier stage than the raninids.

EUBRACHYURA (HETEROTREMATA & THORACOTREMATA)

Guinot's Heterotremata consists of the superfamilies Dorippoidea, Calappoidea, Corystoidea, Portunoidea, Xanthoidea, Majoidea, Parthenopoidea, Bellioidea and Leucosioidea. It therefore corresponds to Milne Edwards' Cyclometopa with the addition of the dorippids (excluding the tymolids), the calappids and the leucosiids from the Oxystomata, and the majids and parthenopids from the Oxyrhyncha. The Thoracotremata contains all the remaining higher crabs and therefore corresponds to Milne Edwards' Catometopa with the addition of the hymenosomatids.

In attempting to categorize the zoeal stages, and having, like Guinot, dismembered the oxystomes and oxyrhynchs, I thought that I could recognize three main groups. The first of these, the majids, seemed to be a well-defined one in which the zoeal phase is abbreviated to only two stages and well-developed pleopods are present in the second stage. The remaining two groups were much less easily distinguished, but each consisted of a series of families in which the zoeal stages were respectively relatively primitive or relatively advanced. The only feature which seemed consistently to separate these two groups was the number of setae on the endopod of the maxilla, the primitive zoeae having six or more setae and the advanced ones five or fewer. Distinguished in this way, the primitive group corresponded to Guinot's Heterotremata except for the Majidae, which were separated as mentioned above, and the Leucosiidae, Dorippidae and perhaps part of the Calappidae which seemed to be allied with the more advanced families. With the addition of these families, the advanced group therefore corresponded to Guinot's Thoracotremata.

I realized that evolution within the higher brachyurans has been far from simple and has probably involved many separate lines. Nevertheless, the apparent existence of these two large groups of crabs with seemingly primitive and advanced zoeae respectively, together with Guinot's recently published thesis, encouraged me to hope that phylogenetic lines might be discernible from one group to the other. In fact, this hope was not realized, for although I was able tentatively to identify some possible phylogenetic lines within the primitive zoeal groups, I was unable to extend these into the more advanced families because many of them seemed to have a confusing mixture of advanced and primitive features which precluded their derivation from any of the extant groups with generally more primitive zoeae.

Adopting the view of eubrachyuran phylogeny suggested by Saint-Laurent, many of these difficulties disappear. For according to this view the Heterotremata and Thoracotremata should be considered as quite distinct taxa with no phylogenetic links between them. On the other hand, this approach poses new problems, for although the zoeae of the Heterotremata are certainly generally more primitive than those of the Thoracotremata, there is much more overlap than I had thought. The distinction between the two groups based on the setation of the endopod of the zoeal maxilla is clearly invalid, for the leucosiids and dorippids are simply highly evolved Heterotremata in which the zoeal morphology has advanced beyond the general level for this group and in a number of features, including the maxilla setation, has approached the thoracotrematous condition. The same is true of the most advanced majids, but in this case a single family, if indeed it is to be regarded as such, contains a whole range of zoeal forms from the relatively primitive oregoninids to the very advanced inachinids.

Having eliminated the maxillary endopod setation as a distinction between the hetero-trematous and thoracotrematous zoeae, I can find no other single feature or combination of features which will consistently separate the two groups. This seems rather surprising if, as Saint-Laurent has suggested, the Heterotremata and Thoracotremata have had separate evolutionary histories from a very early stage. However, the key difference between the two groups, that is whether or not the coxae of the fifth legs are involved with the male reproductive apparatus, would not directly affect the larval stages at all. For although this difference may have resulted in the adults evolving along very diverse adaptive lines, the Heterotremata retaining the benthic habit or becoming at least partly pelagic while several of the thoracotrematous groups have invaded the terrestrial environment, the zoeal stages of both groups have retained the primitive planktonic dispersive role. Under these circum-stances, while the selective pressures operating on the adults might be expected to cause the two groups to diverge in features not directly related to the primary distinction between them, adaptation by their larval stages to the same life-style would presumably result in convergence.

Assuming that my interpretation of primitive and advanced zoeal characters is correct (Rice, 1980a, p. 299 et seq.), such convergence indeed seems to have occurred. Thus, although the most primitive zoeae of the Thoracotremata have a much simpler appendage

setation than most zoeae of the Heterotremata, the same trends are apparent in both groups. In both cases the armature of the carapace and abdomen tends to become reduced, the separation of the sixth abdominal somite from the telson tends to become delayed, the setation of the cephalic appendages tends to become simplified, and there is some fusion of segments, particularly of the endopods of the maxillule and the third maxilliped. As a result of these trends, both sections of the Eubrachyura contain families with at least some representatives having zoeae in which some or all of the carapace spines are absent, the antennae are greatly reduced, the setation of the endopods of the maxillule and maxilla are greatly simplified, the segments of the endopod of the third maxilliped are partly fused and the sixth abdominal somite is fused with the telson throughout the zoeal phase. These conditions are found in the Leucosiidae amongst the Heterotremata and the Pinnotheridae amongst the Thoracotremata, producing a general resemblance between the two which led me to believe that they are closely related (Rice, 1980*b*). The same trends are apparent in a rather less extreme form in the advanced spider crabs (Inachinae) and the Dorippidae amongst the Heterotremata, and in the Hymenosomatidae amongst the Thoracotremata.

However, apart from the advanced features which they share, these groups are all very distinct, four of them, for instance, having the most characteristic telson structures of any of the brachyurans, quite different both from each other and from those found in any other families. They each appear to represent the end point of a different phylogenetic line and suggest that the evolution of each of the sections of the Eubrachyura has involved several of these lines, though not all of them, perhaps, have produced such advanced zoeae. Using only the zoeal characters, in my earlier paper I attempted to trace these lineages amongst the forms which I then considered to be the cyclometopous families, that is the Heterotremata excluding the Leucosiidae and the Dorippidae. Although the philosophy behind this attempt was incorrect in that I hoped to be able to extend the lines into the more advanced zoeal groups, the general conclusions, summarized here in somewhat simplified form in Fig. 3, are still probably valid.

From an ancestral form with a zoea similar to the most primitive of the extant xanthids, two major lines are envisaged, one leading to the Portunidae and Geryonidae and thence to the Parthenopidae, and the other to the Corystidae, Cancridae and part of the Atelecyclidae (that is the Corystoidea of Guinot) possibly via the Calappidae. A third major line, comprising the Majidae, is suggested as having separated from the ancestral stock at a level preceding that represented by the most primitive extant xanthids.

Apart from the Leucosiidae and the Dorippidae, these three major lines together account for most of the Heterotremata. However, several groups of known zoeae do not fit readily into this simple pattern and indicate the existence of a number of subsidiary evolutionary lines. First, anagenesis in several families has resulted in sub-families with zoeal features which suggest that they are offshoots from the main lines. This seems to be true of the Carcininae and Portuninae within the Portunidae, and of the Pilumninae and Xanthinae within the Xanthidae. Within the Cancridae, two distinctly different types of larvae are found in the single genus *Cancer* and, according to the criteria I applied, the Corystidae could have been derived only from the more primitive of these. Secondly, some whole families appear to represent short side-branches; the Geryonidae seem to be an off-shoot from a polybiinid ancestor, while the Goneplacidae seem to be very closely allied to the Pilumninae. Thirdly, some heterotrematous zoeae are so unusual that I can only assume that they represent separate, independent lines. One such group is the Bellidae, regarded as a subfamily of the Atelecyclidae by Balss (1957), but completely separated from the Corystoidea by several authors and given superfamily status by Guinot (1978). In my review I discussed only the larvae of *Corystoides* and *Heterozius,* for at that time I was unaware of the excellent descriptions of the larvae of *Acanthocyclus gayi* Milne Edwards and Lucas by Fagetti & Campodonico (1970) and *Acanthocyclus albatrossis* Rathbun by Campodonico & Guzman (1973). These zoeae resemble those of *Corystoides* in all essential details, including the very unusual setation of the endopod of the second maxilliped, and confirm the necessity of separating the group totally from the Atelecyclidae. Two other genera which
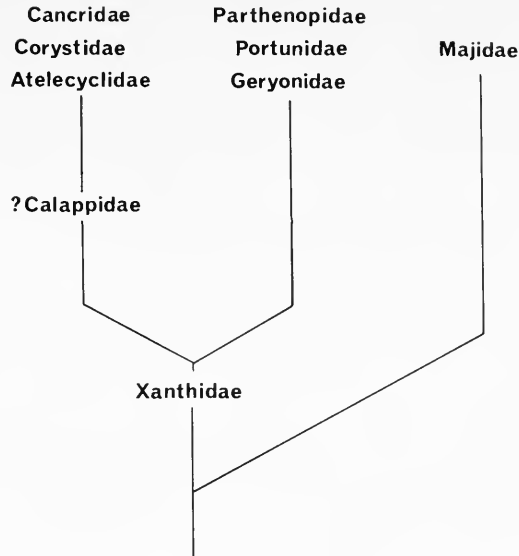
Fig. 3 Main suggested phylogenetic lines within the Heterotremata.

have usually been placed in the Atelecyclidae, *Telmessus* and *Erimacrus,* also have some unusual zoeal features which seem to separate them quite clearly from the remainder of the Corystoidea, but do not obviously ally them with any other group. These features include the appearance of the 'exopod' seta on the maxillule in the first stage, the unusually large number of scaphognathite setae in this stage and the presence of lateral setae on the endopod of the first maxilliped. I was, and am, unable to say where these genera belong, but can only suggest that since some of their zoeal characters indicate that they may have abbreviated a longer ancestral series of zoeal stages, they may have evolved from close to the stock which gave rise to the majids by a similar change in developmental strategy. Finally, the zoeae of the monotypic genus *Orithyia* possess a combination of features quite unlike that of any other known crab. The genus was placed with some doubt in the Calappidae by Ihle (1918) while Guinot (1978) gave it separate family status in her Calappoidea. There is certainly no feature of the zoeae of *Orithyia* which would rule out the possibility of it being derived from the more primitive calappid zoeae such as those of *Calappa* or *Hepatus.* On the other hand, the two groups have little in common which would positively indicate such a relationship. Instead, as I pointed out in the earlier paper, *Orithyia* zoeae have a superficial resemblance to the dorippids in having very long spinulose dorsal and rostral carapace spines and extended telson forks. *Orithyia* and dorippid zoeae also share with the higher majids the rather unusual feature of only three medial setae on the basis of the second maxilliped, while the first zoeal stage in both *Orithyia* and in the spider crabs has rather more marginal setae on the scaphognathite than is usual in the Brachyura. I have linked this last character with the abbreviated development of the majids, and since *Orithyia* passes through only three zoeal stages the same may be true here. However, none of these features indicate any clear relationship for *Orithyia* and I am therefore quite unable to suggest where it belongs.

I am similarly unable to place the Leucosiidae and Dorippidae into this scheme. Their zoeae are generally much more advanced than those of most other heterotrematous families and their specialized features, particularly their telsons, indicate that they occupy rather isolated positions at the ends of heterotrematous evolutionary lines. Since dorippid zoeae consistently have three setae on the basal segment of the endopod of the first maxilliped they presumably could not have been derived from the portunid-parthenopid branch which have only two setae in this position. Otherwise, however, both dorippid and leucosiid zoeae could have evolved from those of any of the heterotrematous groups.

As noted above, in my earlier review I was unable to identify any possible phylogenetic lines within those brachyuran groups with relatively advanced zoeae. This was partly because I had expected to be able to extend the suggested heterotrematous lineages into the Thoracotremata. Treating the Thoracotremata as a distinct group, as I am here, it is still difficult to identify possible evolutionary lines within it, but some general points can be made.

First, the Hymenosomatidae have a number of very advanced zoeal characters which in the past led me to believe that they are fairly closely related to the Pinnotheridae and the Leucosiidae (Rice, 1980a, p. 315). However, since the Leucosiidae are here considered to be advanced Heterotremata, a close relationship between them and the hymenosomatids is precluded. Similarly, although the zoeae of the Hymenosomatidae share with those of the Pinnotheridae a number of advanced features, including reduced carapace spines with the laterals, where present, close to the ventro-lateral margin, reduced antennal exopod, reduced setation of the maxillule and maxilla, and the failure of the sixth abdominal somite to become separated from the telson in all known hymenosomatids and several pinnotherids, the Hymenosomatidae have a number of much less advanced features which argue against a close relationship between the two families. Thus, the proximal segment of the endopod of the maxillule always carries a seta in hymenosomatids but is unarmed in pinnotherids, the endopod of the maxillule carries five setae in the hymenosomatids but only three in the pinnotherids, the endopod of the second maxilliped consists of three segments in the hymenosomatids but only two in the pinnotherids, and the basal segment of the endopod of the first maxilliped carries three setae in the hymenosomatids compared with two in the pinnotherids. In this last feature the Hymenosomatidae are unique amongst the Thoracotremata, suggesting that they could not have evolved from any of the extant groups. On the other hand, hymenosomatids have several very specialized features, particularly the reduced coxal endite on the maxilla, the failure to develop pleopods during the zoeal phase and a total absence of a megalopa stage, which indicate that they could not have been ancestral to any of the other extant groups either. I assume, therefore, that the hymeno-somatids are the sole extant representatives of a thoracotrematous evolutionary line which separated from the remainder at a very early stage.

Like the Hymenosomatidae, the advanced Pinnotheridae have a number of specialized zoeal features, particularly the very characteristic telson, which suggest that no other extant group could have evolved from them. Moreover, all pinnotherid zoeae have the antennal exopod vestigial or absent, the basal segment of the endopod of the maxillule unarmed, only three setae on the endopod of the maxilla, and the endopod of the second maxilliped consisting of only two segments, the proximal being unarmed*. This combination of characters is more advanced than that of any thoracotrematous group and is approached only by the Ocypodinae in which, however, the antennal exopod is rarely rudimentary and the endopod of the second maxilliped always consists of three distinct segments. This resemblance does not, of course, necessarily indicate a close relationship, for there are considerable differences between ocypodinid and pinnotherid zoeae. Nevertheless, the appendage setation is so similar in the two groups that it seems likely that they both evolved from the same, or closely related, ancestors.

The zoeae of the other ocypodid sub-families, that is the Macrophthalminae and the Scopimerinae, are both somewhat less advanced than those of the Ocypodinae. While either of these more primitive sub-families could have given rise to the Ocypodinae, neither of them could apparently have evolved from the other (see Rice, 1980a, p. 344). Either or both of them must therefore be off the postulated line which led to the Ocypodinae and thence to the Pinnotheridae.

A similar situation exists in the Grapsidae from which the Ocypodidae were possibly derived. Here, the subfamily Grapsinae contains the most advanced zoeae, derivable from any of the other sub-families. But the Sesarminae, Plagusinae and Varuninae each have

*When preparing the general review (Rice, 1980a) I was unaware of the description of the larvae of *Pinnixa rathbuni* Sakai by Sekiguchi (1978).

different combinations of advanced and primitive characters which suggest that they each represent a different evolutionary line within the family (see Rice, 1980*a*, p. 340).

Finally, the zoeae of the Gecarcinidae seem to be at an evolutionary level comparable with, or slightly below that of the less advanced sub-families of the Grapsidae and are therefore the most primitive of the known thoracotrematous forms. This does not mean that the gecarcinids are ancestral to the remainder of the Thoracotremata, but it certainly suggests that they separated from the other evolutionary lines before the zoeae of the latter had attained their present forms.

These suggested relationships between the zoeae of the Thoracotremata are far too vague to be formalized into any kind of phylogenetic diagram, even one as tentative as that produced above for the Heterotremata. Nevertheless, they do indicate relative evolutionary levels which may be useful in support of evidence from adult morphology and palaeontology. They also provide a framework to be strengthened or changed as each new piece of larval evidence is obtained, for like all larval studies, they are based on data from only a small proportion of the species known as adults.

Conclusion

Brachyuran zoeae can provide valuable insights into crab relationships at a variety of taxonomic levels. Since they are all adapted for a relatively similar pelagic existence rather than the very varied environments occupied by the adults stages, they may help to separate groups which have been classified together because of a superficial resemblance between the adults caused by convergence. At the highest level this is the case, for instance, of the Oxystomata and the Oxyrhyncha, while at a lower level the example of the Atelecyclidae sensu Balss (1957) might be cited.

However, assuming that Saint-Laurent is correct in her interpretation of the Heterotremata and Thoracotremata as having had quite distinct evolutionary histories, this re-examination of the zoeal data has convinced me of a potential danger in the uncritical use of larval information. For groupings based on the larvae, such as those which I thought were recognizable within the Eubrachyura, may be just as misleading as those based on the adults. A major divergence amongst the adult forms, such as the suggested one between the Heterotremata and the Thoracotremata, may not be reflected in the larval stages since parallel adaptation to the same pelagic life-style may cause the zoeae of advanced members of both branches to share apomorphous characters which have apparently been acquired independently, as in the Leucosiidae and the Pinnotheridae.

There remains the problem of explaining why the thoracotrematous zoeae are generally so much more advanced than those of most of the heterotrematous groups. One explanation might be that the early Thoracotremata, which presumably had zoeae at more or less the same evolutionary level as those of the bulk of the Heterotremata, have left no extant representatives. But this rather begs the question since it does not explain why these forms should have disappeared while the primitive Heterotremata survived.

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